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PRINCIPLES

OF

COMPARATIVE PHYSIOLOGY.

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THIS VOLUME IS

MOST RESPECTFULLY DEDICATED,

AS A TRIBUTE DUE ALIKE

TO

HIS HIGH SCIENTIFIC ATTAINMENTS,

AND MORAL WORTH,

AND AS AN EXPRESSION OF GRATITUDE FOR

THE BENEFIT DERIVED FROM HIS

"DISCOURSE ON THE STUDY OF NATURAL PHILOSOPHY,"

BY

THE AUTHOR.

PREFACE.

"SCIENCE IS THE KNOWLEDGE OF MANY, ORDERLY AND METHODICALLY DIGESTED AND ARRANGED, SO AS TO BECOME ATTAINABLE BY ONE."—*Sir John F. W. Herschel.*

THE success of the Third Edition of the "Principles of Physiology, General and Comparative,"—as evinced, not merely by its rapid sale, but by the numerous expressions of high appreciation which it drew forth from those most competent to judge of its merits,—has encouraged the Author to carry into effect a change of plan which had suggested itself to him during its preparation. For having been led-on by the desire of rendering his work as complete as possible, to enlarge it to the utmost admissible dimensions of a single volume, he felt that it would be impossible to do justice to any subsequent extensions which its subject might receive, without making some alteration in its form. And this conclusion acquired a greatly-increased force, when the demand for a new Edition led him to survey the deficiencies, which, notwithstanding all his care, had been left in the former one; and to estimate the amount of new matter, not only deserving but requiring notice, which the diligence of observers in various departments of this comprehensive Science had accumulated in the short interval. Instead of dividing the entire Treatise into two Volumes, however, as suggested to him by many of his friends, the Author has preferred to divide its *subjects*, and to treat of them separately though connectedly.

The present Volume, therefore, consists of the "Comparative Physiology" of the last Edition, extended from 530 pages to 744, and with 300 illustrations instead of 130. The First Chapter (the Eighth of the former Edition) has been entirely re-written, with the view of bringing into greater prominence the general doctrine of *Progress from the General to the Special;* the enunciation of which by Von Baer (nearly thirty years ago) appears to the Author to mark a most important era in the Philosophy of Physiology, although it is far from having received the notice which it deserved from various subsequent writers who have followed in the same track. The principal additions and alterations in the succeeding Chapters (as to the general arrangement of which no change has been found necessary) occur in the part of Chapter VI. which relates to the Water-Vascular System, and in the part of Chapter XI. which treats of the Sexuality of the Cryptogamia; in regard to which latter point the Author would observe, that the course of recent discovery has fully borne-out the anticipations he expressed in the former edition. The whole work, however, has been most carefully revised; and the Author ventures to think that the present Edition more completely represents the state of the Science at the period of its publication, than any of its predecessors have done. He can honestly say that he has spared no time or labour in its preparation, which it has been in his power to bestow. And he looks with hope, therefore, to a continuance of that friendly indulgence with regard to errors and shortcomings, which has been so liberally afforded on previous occasions. As to certain points on which his opinions have undergone modification, he can again refer with satisfaction to the following passage in the Preface to his former editions:—"*Truth* is his only object; and, even if his own doctrines should be overthrown by more extended researches, he will rejoice in their demolition, as he would in that of any other error. The character of the true philosopher as described by Schiller,—*one who has always loved truth better than his system,*—will ever, he trusts, be the goal of his intellectual ambition."

In attempting to embody in a Systematic Treatise the general aspect of Physiology or any other Science of like comprehensiveness, it will be obvious that an Author, however extensive his own range of acquirement, must largely avail himself of the labours of others; and that the scientific character of such a treatise must depend, not so much on the amount of original matter it may contain, as on the degree in which "the knowledge of many" has been "orderly and methodically digested and arranged, so as to become attainable by one." It is by this standard that the Author desires his work to be tried; and he cheerfully leaves the verdict to the judgment of those, who are qualified by their own knowledge of the subject to pronounce it. He feels it due to himself, however, to state that he has devoted considerable time and attention to the verification of the statements of other observers, especially on points under dispute,—a kind of labour which is but little appreciated by those, who contemptuously designate works like the present as "mere compilations;" and that a large amount of materials, drawn from his own original enquiries, is scattered through the work. It would have been easy for him to bring these last into greater prominence, had he been so disposed; but as his constant aim has been, to work-out his general plan harmoniously and methodically, rather than to force any one portion of it into undue prominence, he has generally preferred to allow his own contributions to pass undistinguished, rather than to be continually obtruding his personal claims upon the attention of his readers. He would remark, moreover, that originality may be as much shown in the development of new relations between facts and phenomena observed by others, as in the first discovery of such facts; and he believes that by the mode in which he has combined and arranged his materials, he has frequently been enabled to impart a new and unexpected value to statements, which, in their previously isolated condition, were of comparatively insignificant import.

Although, in the selection of these materials, the Author has endeavoured to avail himself of the best and most recent information he could procure upon each department of the subject, it is scarcely to be expected that he should be equally well-informed upon every point; and those who have followed particular departments into detail, will doubtless find scope for criticism in what they may regard as deficiencies, or even as errors. Here, again, the Author must beg that his work may be estimated by its *general* merits; and rather by what it *does*, than by what it *does not* contain. It would have been far easier to expand it by mere compilation to twice its present dimensions, than it has been found to compress the accumulated mass within the space which it even now occupies.

It has been the Author's endeavour, wherever practicable, to draw the materials, both for his text and for its illustrations, *direct* from original Treatises and Monographs; and thus to avoid the errors which too frequently arise from second-hand transmission. To have attempted, however, to assign each individual fact to its original discoverer, each doctrine to its first enunciator, would have augmented the bulk of the volume far beyond the dimensions appropriate to a Text-Book; and while most desirous to avoid taking credit for what is not his own, the Author has felt himself compelled to limit his references, for the most part, to those *new* facts and doctrines, which cannot be yet said to have become part of the common stock of Physiological Science. The number of such references has been largely increased in the present edition; and the "Index of Authors" which has been added, will, it is hoped, be found useful in enabling the reader at once to turn to the notice of any original observation that he may desire to retrace. The Illustrations not his own, which likewise have received numerous important additions, are referred to their originals in the list at the commencement of the Volume; and this list will also afford useful assistance to those, who may desire to carry-out their enquiries in any particular direction.

The Author cannot bring his task to a conclusion, without expressing the great obligations under which he lies to his friend Mr. T. H. Huxley, not only for many valuable suggestions, but also for the readiness which he has on all occasions evinced, to impart to him whatever he might seek from his own extensive stores of original and acquired information; nor without paying his tribute of regard to the memory of his lamented friend Mr. G. Newport, whose premature death has deprived British Science of one of its most ardent and disinterested votaries, at a time when he was beginning to reap, in the appreciation of his discoveries on the Impregnation of the Amphibia,* the credit so justly due to his laborious, accurate, and sagacious researches, in the new field to the cultivation of which he had latterly applied himself.

It is the Author's intention to reproduce the "General Physiology" of his former Edition, as a companion-volume to the present, so soon as the numerous demands upon his time may permit him to bestow upon that part of his revision the careful attention which it requires.

UNIVERSITY HALL, LONDON,
JUNE 1, 1854.

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* In a Postscript to the work referred-to in the note to p. 536, written almost contemporaneously with Mr. Newport's decease, Prof. Bischoff states that he has himself confirmed Mr. N.'s observation of the penetration of the Spermatozoon into the ovum of the Frog, and gives him full credit for the determination of this important fact.

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CHAPTER I.

ON THE GENERAL PLAN OF ORGANIC STRUCTURE AND DEVELOPMENT.

1. THERE are few things more interesting to those who feel pleasure in watching the extraordinary advancement of knowledge at the present time, than the rapid progress of philosophical views in every department of Biological Science; the pursuit of which has until recently been made to consist, almost exclusively, in the mere collection and accumulation of *facts*, with scarcely any attempt at the discovery of the *ideas* of which they are but the expressions. The laws of *Life* were long considered beyond the reach of human investigation; and the mind shrank from attempting to analyse its complex and varied phenomena, which, though constantly under observation, must be reduced to their simplest form, before any inductive reasoning can be founded upon them. It is recorded, however, of Newton, that, whilst contemplating the simplicity and harmony of the plan according to which the Universe is governed, as manifested in the relations which his gigantic mind discovered between the distant and apparently-unconnected masses of the solar system, his thoughts glanced towards the organised creation; and reflecting that the wonderful structure and arrangement which it exhibits, present in no less a degree the indications of the order and perfection which can result from Omnipotence alone, he remarked, "I cannot doubt that the structure of animals is governed by principles of similar uniformity." ("Idemque dici possit de uniformitate illâ, quæ est in corporibus animalium.") "Why," asks Cuvier in his eloquent discourse on the revolutions of the globe, "should not Natural History some day have its Newton?"

2. Although the labours of the Naturalist and Comparative Anatomist have not yet unveiled more than a small part of that general plan, the complete discovery of which may perhaps be reserved for another Newton, many subordinate principles have been based on a solid foundation, and many more, which were at first doubtful, are daily receiving fresh confirmation. Several of these laws are alike important from their extensive range, and interesting from the unexpected nature of the results to which they frequently lead; and though their application may sometimes appear forced, and inconsistent with the usual simplicity of Nature, further investigation will generally show that the difficulty is more apparent than real,—frequently arising solely from our own prejudices, and diminishing in proportion as we fix our attention upon that *combination of unity of*

plan with variety of purpose, by which is produced the endless diversity united with harmony of forms, so remarkable in the animated world.

3. In comparing phenomena of any kind, for the purpose of arriving at a principle common to them all, it is necessary to feel certain that they are of a *similar character.* Indeed the sagacity of the philosopher is often more displayed in his discovery of that relation amongst his facts, which allows of their being compared together, than in the inferences to which such comparison leads him. The brilliancy of Newton's genius was shown in the perception, that the fall of a stone to the earth, and the motion of the moon around it, were comprehensible under the same law; not in the mere deduction of the numerical law from the ratios supplied by those facts.—In the sciences which have Life for their subject, the apparent dissimilarity of the facts which are made the objects of comparison, often prevents the true relation between them from being readily detected. Here it is that the mental training which the previous cultivation of Physical science affords, becomes peculiarly valuable to the Physiologist. "The most important part of the process of Induction," says Professor Powell,* "consists in seizing upon the probable connecting relation, by which we can extend what we observe in a few cases to all. In proportion to the justness of this assumption, and the correctness of our judgment in tracing and adopting it, will the induction be successful. The analogies to be pursued must be those suggested from already-ascertained laws and relations. Thus, in proportion to the extent of the inquirer's previous knowledge of such relations subsisting in other parts of Nature, will be his means of guidance to a correct train of inference in that before him. And he who has, even to a limited extent, been led to observe the connection between one class of physical truths and another, will almost unconsciously acquire a tendency to perceive such relations among the facts continually presented to him. And the more extensive his acquaintance with Nature, the more firmly is he impressed with the belief that some such relation must subsist in all cases, however limited a portion of it he may be able actually to trace. It is by the exercise of unusual skill in this way, that the greatest philosophers have been able to achieve their triumphs in the reduction of facts under the dominion of general laws."

4. The first group of phenomena encountered by the Biological student, is that presented in the many hundred-thousand diverse forms of organic structure, of which the Animal and Vegetable kingdoms are made up; and it is necessary, at the very outset of the inquiry, to settle the principles upon which these are to be compared. In many instances, it is true, there can be no room for hesitation; the general type of conformation of two or more organisms being obviously the same, and the differences in detail never obscuring the resemblances between their component parts. But this holds good to only a very limited extent; and we are soon forced to recognise such essential differences, alike in the general types of conformation, and in the form and structure of the component parts, that we feel the need of some guiding principle according to which we may arrange these phenomena for comparison.—Now from the time of Aristotle, downwards to the commencement of the present century,

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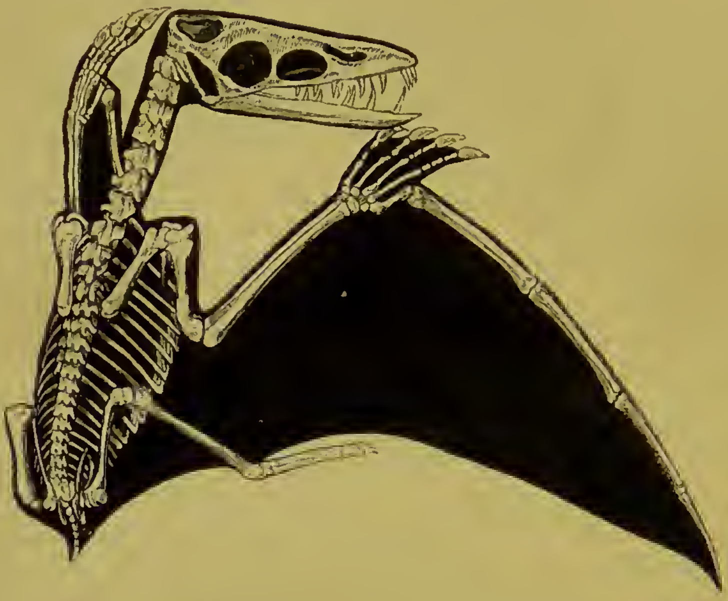
* "Connection of Natural and Divine Truth," p. 33.

Anatomists were in the habit of regarding similarity in external form and in evident purpose, as indicating the analogies between different parts. But although this mode of estimating the character of organs is perfectly correct, when they are considered as *instrumental structures*,—that is, when we are inquiring into the conditions of the function performed by them,—it totally fails, when we are in search of the *plan of organisation*, according to which their evolution has taken place; since it is frequently found that two organs which are not unlike in external form, and which have corresponding functions in the system, originate from elements entirely different, and are therefore fundamentally dissimilar; whilst, on the other hand, organs which at first sight present little or no resemblance to each other, and are applied to very different purposes in the economy, may be really modifications of the same fundamental components.

5. If, for example, we take a cursory glance at the organs of support or motion in the air, with which different Animals are furnished, we shall observe a community of function, and a general similarity of external form, concealing a total diversity of internal structure and of essential character. Amongst all the classes which are adapted for atmospheric respiration, we encounter groups of greater or less extent, in which the resistance of this element becomes the principal means of progression; and even among aquatic animals, there are instances in which the function of locomotion is partly dependent upon the same agency. Wherever *true wings* exist among the Vertebrata, some modification of the anterior member serves as their basis; but there is considerable variety in the mode in which the apparatus is constructed. Thus, in the *Bat* (Fig. 2, E), the required area for the surface of the wing is formed by an extension of the skin over a system of bones, of which those of the hand form by far the largest part; and this membrane is extended also from the posterior extremity, and is attached to the whole length of the trunk, as well as to the tail where one exists. In the *Bird* (Fig. 2, B), on the contrary, the wing is formed by the skin and its appendages attached to the anterior member alone; and here the bones of the hand are developed in a comparatively slight degree, those of the arm and fore-arm being the principal support of the expansion. From what is preserved of the *Pterodactylus*, it seems that the wing of this extraordinary animal was extended, not over the whole member as in the Bird, nor over the hand as in the Bat, but over one of the fingers only, which was immensely elongated in proportion to the rest (Fig. 1). In the *Flying-fish*, again, the pectoral fins may be regarded as, in some sort, its wings (though it does not appear that the animal has the power of raising itself by means of their action on the air, the impulse being given at the moment of quitting the water); these fins evidently represent the anterior members of higher Vertebrata; but the bones of the arm and fore-arm are scarcely developed, while the hand is expanded, and joined immediately, as it were, to the trunk.—A very different structure prevails among those imperfect wings, which serve rather to *support* the animals which possess them, in their movements through the air, than to *propel* them in that medium. Thus, in the *Flying Squirrels*, *Flying Lemurs*, and *Phalangers* or 'flying opossums,' there is an extension of the skin between the fore and hind legs, which, by acting as a parachute, enables these animals to descend with

safety from considerable heights: in the *Draco volans*, on the other hand, the wings are affixed to the sides of the back, being supported by prolongations of the ribs, and are quite independent of the extremities. Here we have still the same function and general form; but it would evidently be absurd to say that the organs are of the same structural character.—A still greater departure from the type with which we are familiar among the higher animals, is presented by the wings of *Insects;* for these are formed by an extension of the superficial tegumentary membrane over a framework that is not derived from an *internal* osseous skeleton, but is an extension of the denser subjacent layer of the *external* integument; and this framework is penetrated, throughout its ramifications, by 'tracheæ' or air-tubes, communicating with those of the interior of the body, and also (at least in the early state of these organs) by vessels or passages for the circulation of blood. As regards their essential structure, in fact, these wings correspond closely with the external respiratory organs with which certain aquatic Larvæ (as that of the *Ephemera*) are provided; and hence they have been not inappropriately designated by Oken as 'aerial gills.'* They may, in fact, be regarded as an excessively developed form of those external appendages of the lower Articulata, which are subservient to locomotion and to respiration jointly; and it is a very interesting example of the similarity of modification which very different plans of structure may undergo, when a common purpose is to

FIG. 1.



Pterodactylus crassirostris.

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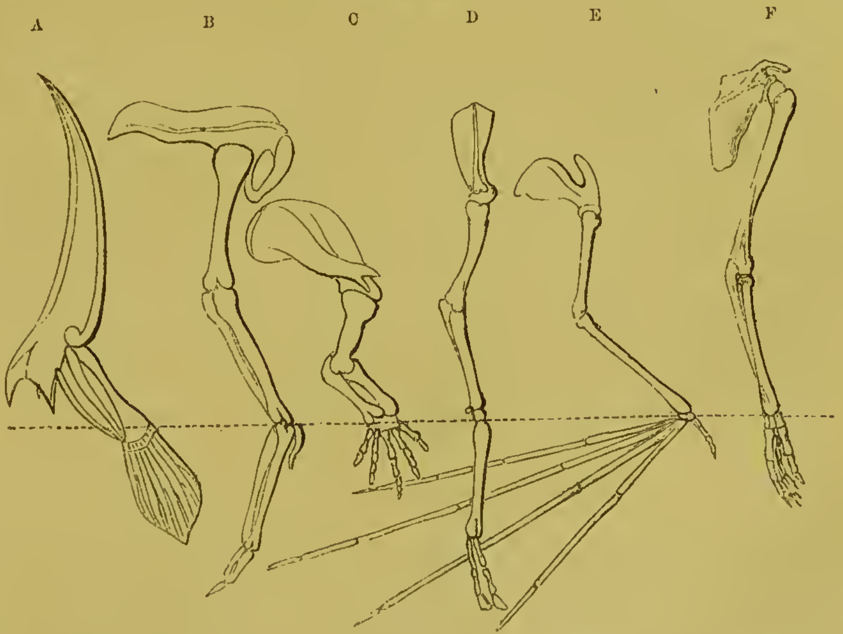
* The attempts of a generation of Entomologists now passing away, under the influence of the erroneous idea already referred-to (§ 4), at bringing into comparison, as similar organs, the wings of Insects, and the anterior members of the flying Vertebrata, can now only excite a smile on the part of the Philosophical Anatomist. Such attempts, however, have exercised a most injurious influence on the progress of science, by drawing off the attention of Naturalists from the true method of philosophical research.

be fulfilled, that, in the wing of the Bird, as well as in that of the Insect, there should be a special prolongation of the respiratory passages into the framework which supports it.

6. Many similar examples might readily be adduced from the Animal kingdom; but the Vegetable world affords them in even greater abundance. To take a very simple case;—the expanded foliaceous surface through which the Plant obtains from the atmosphere the principal part of the solid materials of its growth, though usually afforded by the leaves, which are appendages to the axis developed for this express purpose, is sometimes provided, as in the *Cactaceæ*, by the extension of the surface of the stem itself, which remains soft and succulent; whilst in many of the *Acacias* of New Holland, as in the sub-aquatic leaves of the *Sagittaria* of this country, it is given by the laminal compression of the petiole or leaf-stalk. So, again, the *tendril*, which is an organ developed for the purpose of supporting the plant by twining round some neighbouring prop, is in the *Vine* a transformation of the peduncle or flower-stalk, in the *Pea* a prolongation of the petiole or leaf-stalk, in the *Cucumber* a transformation of the stipule, and in *Gloriosa* the point of the leaf itself; whilst in the singular genus *Strophanthus*, it is actually the point of the petal which becomes a tendril and twines round other parts.

7. We can scarcely select any example of diversity of external conformation and of function, superinduced upon an essential unity of organization, so appropriate as that which is afforded by the comparison of those different modifications of the limbs or members, and especially of the *anterior* pair, by which the several species of Vertebrated animals are adapted to the most diversified modes of life. No Comparative Anatomist has the slightest hesitation in admitting that the pectoral fin of a Fish (Fig. 2, A), the wing of a Bird (B), the paddle of a Dolphin (C), the fore-

FIG. 2.



Different forms of *Anterior Member* :—A, Fish; B, Bird; C, Dolphin; D, Deer; E, Bat; F, Man.

leg of a Deer (D), the wing of a Bat (E), and the arm of a man (F), are the same organs, notwithstanding that their forms are so varied, and the uses to which they are applied so unlike each other. For all these organs not only occupy the same position in the fabric, but are developed after the same manner; and when their osseous frame-work is examined, it is found to be composed of parts which are strictly comparable one with another, although varying in number and in relative proportion. Thus, commencing from the shoulder-joint, we can almost everywhere recognize without difficulty the *humerus*, it being only in Fishes that this is so little developed as not to intervene between the scapula and the bones of the fore-arm; next we have the *radius* and *ulna*, whose presence is always distinguishable, although one of them may be in only a rudimentary condition; then, beneath the wrist-joint (through which a dotted line is drawn in the figure), we find the bones of the *carpus*, which are normally ten in number, forming two rows, but which may be reduced by non-development to any smaller number—three, two, or even one; next, we find the *metacarpal bones*, which are normally five, but are sometimes reduced among the higher vertebrata to four, three, two, or one, whilst in Fishes they may be multiplied to the number of twenty or more; and lastly we have the *digital* bones, of which there are normally five sets, each consisting of three or more phalanges, but which are subject to the same reduction or multiplication as the metacarpal.—It is entirely from the differences of conformation which these osseous elements gradually come to present in the course of their development, that those special adaptations arise, which fit their combination in each case for the wants of the particular species that possesses it; enabling it to be used as an instrument for terrestrial, aquatic, or aerial progression, for swimming and diving, for walking and running, for climbing and flying, for burrowing and tearing, or for that combination of refined and varied manipulations which renders the hand of Man capable of serving as the instrument wherewith to execute the conceptions of his fertile intellect.

8. We may have recourse to the Respiratory system, for another instance, which will bring the contrast between *functional* similarity, or *analogy*, and *organic* correspondence, or *homology*,* into clear view.—An uninstructed observer would scarcely perceive any resemblance between the gills of a Fish (Fig. 145), and the lungs of a Quadruped (Fig. 154), or between the elegant tufts on the head of a Sabella (Fig. 144), and the air-tubes ramifying through the body of an Insect (Fig. 149); and those who are in the habit of forming exclusive notions upon a hasty survey, might be led to deny that any real analogy could exist. When the character of

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* In earlier editions of this work, the terms *functional* and *structural analogy* were used to express the mutual relation of parts, on the one hand as *instrumental structures*, on the other as *fundamentally* or *organically correspondent*. It will be found convenient to limit (as Prof. Owen has done) the use of the term *Analogy* to functional resemblance, and to employ *Homology* as indicative of structural correspondence. Thus by Analogue we now understand "a part or organ in one animal, which has the same function as another part or organ in a different animal:" whilst by Homologue is implied "the same organ in different animals under every variety of form and function." (Prof. Owen's "Hunterian Lectures," Vol. I. Glossary.) Thus, for example, the wing of an Insect is the analogue of that of a Bat or Bird, but not the homologue; whilst the latter is homologous with the arm of Man, the fore-leg of a Quadruped, and the pectoral fin of a Fish.

the function is investigated, however, with the structure which it requires for its performance, it becomes evident that, in order to bring the circulating fluid into the due relation with the atmosphere, all that is needed is a permeable membrane, which shall be in contact with the air on one side, and with the fluid on the other. And this key, applied to the examination of the several forms of respiratory apparatus which exist in the Animal kingdom, shows that they all possess the same essential nature as instrumental structures, and that their modifications in particular instances (which will hereafter be specially described) are only to adapt them to the plan and conditions of the organism at large. There is therefore, *functionally* considered, a relationship of *analogy* amongst all these organs; although they are not really the *homologues* of one another. Thus, the gills of the Fish, and the branchial tufts of the Sabella, are external prolongations of the tegumentary surface, whilst the tracheæ of the Insect, and the lungs of air-breathing Vertebrata, are internal reflexions of that surface; and farther, the two former sets of organs, as the two latter, differ from each other in regard to the *part* of the surface from which the prolongation or inversion takes place. In the *Perennibranchiate Batrachia,* moreover, both lungs and gills are present; and their essential difference of character is most apparent, whilst their correspondence as instruments of the same functional operations is equally evident. Further, in the air-bladder of the Fish, we have an apparently anomalous organ, the only known use of which is to assist in locomotion; yet when a comparison is made between its most developed forms and the simplest pulmonary sacs of Amphibia, no doubt can remain that it is to be regarded as a rudimentary lung; and the study of its development leads to the same conclusion. (See CHAP. VI.)

9. It would be easy to adduce numerous parallel examples from the Vegetable kingdom; wherein organs which correspond in structure, connections, and development, and which are therefore *homologous,* are observed to assume the most varied forms, and to perform the most different functions. It will be sufficient, however, to advert to the well-known fact, that the underground 'creeping roots' (as they are commonly accounted) of the Couch-grass, the subterranean 'tuber' of the Potato, the 'rhizoma' or 'root-stalk' of the Iris, the solid 'cormus' of the Colchicum, the 'bulb' of the Hyacinth, and the 'runner' of the Strawberry, are not less truly *stems,* than are the lofty trunks of the Palm or Elm, notwithstanding the variety in their form, texture, and mode of growth; for they all constitute the *ascending axes* of the Plants of which they respectively form part, and have the power of developing the foliaceous appendages which become leaves or flowers, whilst the radical fibres, which constitute the essential part of the roots, grow downwards from their base.

10. In all these cases, we might with perfect propriety found any inquiries regarding the *functional power* of the organs respectively compared, upon their capacity as instruments adapted for a particular purpose. For example, we might estimate the respective force with which Birds, Bats, and Insects, could be propelled through the air, by ascertaining the superficial area of their wings, and the energy and rapidity with which these are moved; or we might judge of the respiratory power of an Animal or Plant, by the extent of surface through which the nutritive

fluid comes into relation with the atmosphere, by whatever portion of the fabric that surface might be afforded. But the Philosophical Anatomist, who seeks to determine the *organic relation* of these parts, must first consider their internal conformation, and examine into the *structural elements* of which they are composed. In the cases just alluded to, he would find not merely the osseous elements, but the muscles, nerves, blood-vessels, &c., presenting essentially the same disposition in the arm of Man, the fore-leg of the Quadruped, or the wing of the Bat or Bird. But on passing to the Insect, he would encounter, as we have seen, an entire change in the plan of structure; the same purpose being fulfilled by instrumental means of a very different order, corresponding, in fact, to those which in the Articulata generally are made subservient to the respiratory process.—The next step in the determination of homologies, is to trace the *connections* of the organs compared, which frequently enables the real nature of parts to be recognized, which would be otherwise obscure. For it is a principle of very extensive application, that similar parts are connected with similar parts, in different animals of the same type. Thus, we never find a hand or foot springing directly from the spinal column of a Vertebrate animal; the connection being always established by other bones, which, whatever may be the variety in their size and shape, are never wholly wanting. Hence, where we find, as in the Fish, the hand excessively developed, and no external trace of an arm or fore-arm, we expect to find it supported internally by a radius and ulna, and these again to be connected with the scapular arch by the intermediation of a humerus. Now the bones of the fore-arm are generally distinctly developed, whilst the humerus very commonly coalesces with the coracoid, so that its presence might be easily overlooked; yet even this is found in certain species to be present as a separate bone.*—Great assistance, again, in the determination of the homologies of organs, is afforded by the examination of *transitional* or *intermediate forms.* Thus, it has been by the regular progression exhibited in the structure of the pulmonic apparatus, from the simple, closed, undivided air-sac of most Fishes, through the higher forms which this organ presents even in that class, and through the various phases which it exhibits in the Perennibranchiate Batrachia, that the homology of the swimming-bladder of the Fish with the lung of the air-breathing Vertebrata has been established. In like manner, it has been by tracing-out the intermediate forms of the bones of the extremities (Fig. 3, B, D), that Prof. Owen has succeeded in proving the complex limbs of the higher Vertebrata, to be homologous with the simple rod-like members (A, C) of the *Lepidosiren* (Fig. 150); whilst these last serve as the connecting-link, whereby the homology of the scapular and pelvic arches with the hæmal or visceral arches of other vertebral segments is indicated; the bones of the limbs being at the same time shown to be homologous with their 'diverging appendages' (of which we have examples in the backward projections that spring from the ribs of Birds), and the scapular arch with its anterior members being thus found

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* See Prof. Owen's "Lectures on Comparative Anatomy," Vol. II. p. 120. The two bones supporting the Fin in Fig. 2, A, are considered by Prof. Owen to be elongated carpals, not (as usually supposed) radius and ulna. If this be the case, the member should have been so placed in the figure, that the dotted line which marks the place of the wrist-joint should have passed *above* instead of *below* them.

to be the completion of the occipital segment, whose centrum and neural arch enter into the composition of the cranium. So, again, the identity of

Fig. 3.

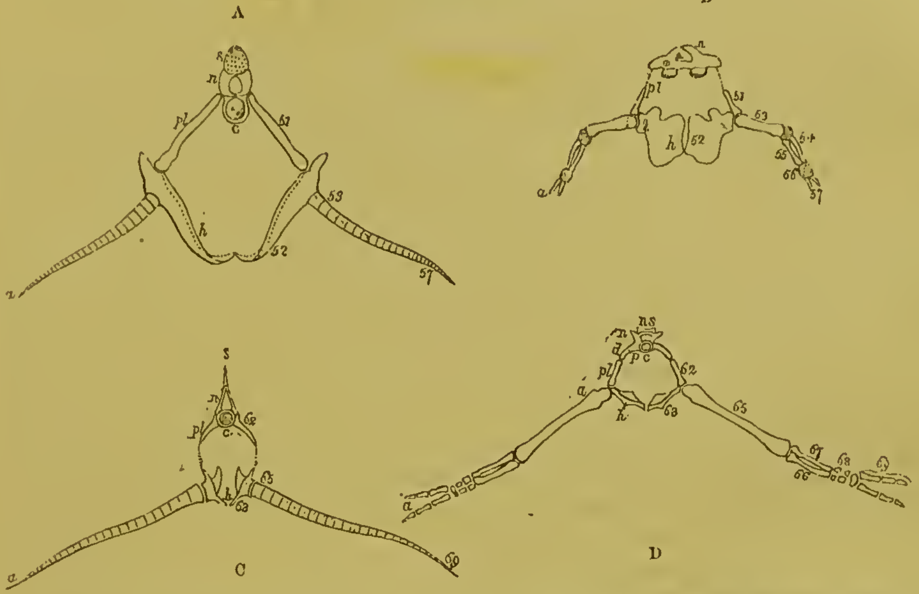

Diagram illustrating the *Nature of Limbs*:—A, posterior view of the occipital vertebra of *Lepidosiren annectens*:—B, posterior view of the occipital vertebra of *Amphiuma didactylum*:—C, posterior view of the pelvic vertebra of *Lepidosiren*:—D, posterior view of the pelvic vertebra of *Proteus anguinus*. In the several diagrams, the following references indicate corresponding parts; *c*, centrum; *n*, neurapophyses; *s*, neural spine; *pl*, 51, pleurapophysis of the occipital vertebra, or scapula; *h*, 52, hæmapophysis of the occipital vertebra, or coracoid bone; *a*, 53-57, diverging appendages of the occipital vertebra, or anterior limbs; *pl*, 62, pleurapophysis of the pelvic vertebra, or iliac bone; *h*, 63, hæmapophysis of the pelvic vertebra, or ischiac bone; *a*, 65-69, diverging appendages of the pelvic vertebra, or posterior limbs.

composition between the jaws and the true legs of the Crustacea, is shown by the transitional gradations presented by the feet-jaws. And turning to the Vegetable kingdom, we find the mutual relations of the parts of the flower, and their homology with the leaves, to be indicated by those cases in which there is a gradational passage from the leaf to the bract, from the bract to the sepal, from the sepal to the petal, from the petal to the stamen, and from the foliaceous type to the carpel (§ 30).—But it is most certain that, of all the means of discovering the structural relations of organs, the study of their *development* is most important; since this, if carefully pursued, will probably never fail to clear up whatever doubts may be left by other modes of investigation. It is in this manner that the true solution has been at last attained, of many of the most difficult and most controverted questions in the science;—questions which have reference, not merely to the nature of particular organs, but to the relations subsisting between different groups of living beings. And it is in this path, therefore, that the Philosophic Naturalist can press forward with the most assured prospect of success, in the search for that *general plan* of Organisation, which it is his highest object to discover.

11. Thus we are led by the study of *Morphology* (that is, by the recognition of 'homologous' organs, under whatever forms they may present), to the perception of that great general truth, which is, perhaps, the highest yet attained in the science of Organisation, and which is even yet

far from being fully developed; that in the several tribes of organised beings, we have *not* a mere aggregation of individuals, each formed upon an independent model, and presenting a type of structure peculiar to itself; but that we may trace throughout each assemblage *a conformity to a general plan,* which may be expressed in an 'archetype' or ideal model,* and of which every modification has reference either to the peculiar conditions under which the race is destined to exist, or to its relations to other beings. Of these special modifications, again, the most important themselves present a conformity to a plan of less generality; those next in order to a plan of still more limited extent: and so on, until we reach those which are peculiar to the individual itself. This, in fact, is the philosophic expression of the whole science of Classification. For, to take the Vertebrate series as our illustration, we find that Fishes, Reptiles, Birds, and Mammals agree in certain leading features of their structure, which constitute them *vertebrated* animals; but this structure is displayed under diversified aspects in these *classes* respectively, which constitute their distinctive attributes. Thus, of the *general* vertebrated type, the Fish presents one set of *special* modifications, adapting it to its peculiar mode of life; the Reptile, another; the Bird, a third; the Mammal, a fourth. So again, in each of these classes, we find its general type presenting subordinate modifications in the respective *orders;* thus, for example, the Reptilian type exhibits itself under the diverse aspects of the Frog, the Snake, the Lizard, and the Turtle; the Mammalian, under those of the Whale and the Bat, the Sloth and the Deer, the Elephant and the Tiger, the Kangaroo and the Monkey, the Ornithorhyncus and Man. Each order, again, is subdivided into *families,* in accordance with the subordinate or more special modifications which the type of the order presents; every one of these families displaying the type of the class and order, with distinctive variations of its own. Each family consists of *genera,* in every one of which the family type is presented under a somewhat diversified aspect. Each genus is made up of an aggregation of *species,* which exhibit the generic character under a variety of modifications; these, however slight, being uniformly repeated through successive generations. Lastly, each species is composed of an assemblage of *individuals,* every one of which repeats the type of its kingdom, subkingdom, class, order, family, genus, and species, through its whole line of descent.

12. Thus, in assigning to any particular being its place in the Organised Creation, we have to proceed *from the general to the special.*—We will suppose an unknown body to be brought for our determination; the first business is to ascertain whether it be an Organised fabric, or a mass of Inorganic matter. This is soon discriminated, in the majority of cases, by an appeal to those *most general* characters which distinguish *all* organised structures from inorganic masses; and the next question is to determine its Animal or Vegetable nature, by the aid of those characters which are not common to both, but are distinctive of each respectively. We will suppose the Animal nature of our unknown body to have been ascertained; the question next arises, to which of the four sub-kingdoms

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* For an admirable exposition of this doctrine, as it respects the osseous system of Vertebrated Animals, see Prof. Owen's treatise on "The Archetype and Homologies of the Vertebrate Skeleton."

it shall be referred; and this, again, has to be ascertained by an appeal to characters which are less general than the preceding, not being common to all organised structures, nor yet to all animals, but being restricted to each of the four sub-kingdoms respectively. Then having ascertained that it is a Vertebrated, Molluscous, Articulated, or Radiated animal, as the case might be, the Naturalist would determine its order by characters of still less generality, which are peculiar to that order; its family, by features which are still more limited; its genus, by those modifications of family character which are presented by the several genera it includes; and lastly, its species, by characters which are the most special of all, that is, which are limited to that race alone.

13. Now if our classification were perfect, it would be comparatively easy to determine the 'archetype' or ideal model of each group; because we should have all the forms before us, by the comparison of which the Philosophical Zoologist seeks to educe what is common to the whole. But in practice it has often been found extremely difficult to determine what shall be considered as characters of classes, what of orders, and so on; since their respective values are very commonly mistaken by those who are imperfectly acquainted with the true principles of classification, and sometimes even by the instructed Naturalist. Thus in popular ideas, a Bat ranks as a Bird, because it flies by wings through the air; whilst the Whale ranks as a Fish, on account of its fish-like form, habitation, and mode of progression. But the scientific Zoologist has no hesitation in placing the Bat amongst the Mammalia, because it presents all the characters which are essential to that class, and which distinguish it from that of Birds; namely its viviparous and placental generation, its subsequent nurture of its young by lactation, its covering of hair, the dental armature of its mouth, its diaphragmatic respiration, its highly-developed cerebrum, and many other peculiarities of conformation; whilst its apparent resemblance to the class of Birds merely results from the adaptation of the Mammalian type to an aerial life. So, again, notwithstanding its fish-like habits, and the peculiarities of structure which adapt it to these, the Whale is a Mammal in all which is essentially characteristic of the class, and which distinguishes it from that of Fishes; namely, its atmospheric respiration, its complete double circulation, its warm blood, its viviparous generation and subsequent lactation, its well-developed cerebrum, its osteological and many other peculiarities.—Here, then, the determination is easy to those who possess but a smattering of Zoological knowledge. But we will take another case, in which a fundamental error was committed even by a great Master in modern science, owing to his misapprehension of the value of characters. Following too closely the indications afforded by the teeth (which are valuable in so far only as they serve as a key to the general plan of conformation), Cuvier placed the *Marsupial Mammalia* in the first instance as a subdivision of his order *Carnaria;* and even when he subsequently raised them to the rank of a distinct order, he gave them a position intermediate between the Carnaria and the Rodentia. Likewise, on account of the absence of teeth, he associated the *Monotremata* with the Sloths and Ant-eaters, in his order Edentata; satisfying himself with indicating that they presented a certain degree of affinity to the Marsupiata. Now the mutual resemblance of these two orders is extremely close; and their unlikeness to all other Mammalia, in the

structure of their cerebrum, and in the mode in which the genital function is performed (two characters of fundamental importance), is such as unquestionably to require their detachment as a distinct subclass.—So, again, it is now coming to be perceived, that the adaptation of the Mammalian structure to a fish-like habit of life, is not of itself sufficient to assemble all the animals which present it into a distinct order; for whilst the greater part of those which agree in possessing the Cetacean form, agree also in structure and carnivorous habit, there are certain genera (the *Dugong, Manatee*, and *Stellerine*) which have been until recently ranked with them, but which are found rather to correspond in the more essential peculiarities of their organisation with the great series of *herbivorous* Mammals, and to be connected with that series by forms now extinct.

14. Many other examples might be cited, illustrative of this difficulty, which is one that especially presents itself among the lower classes of animals, with whose structure and physiology the acquaintance of the Naturalist is as yet very imperfect. It is one, however, which is continually lessening with the progress of research; and whilst, therefore, we should avoid placing too much confidence in existing systems of classification, and in existing ideas of what really constitute natural groups, we may look forwards with hope, if not with absolute confidence, to the gradual accumulation of those materials, which shall enable the Philosophic Naturalist to do that for each group, which has been already

Fig. 4.

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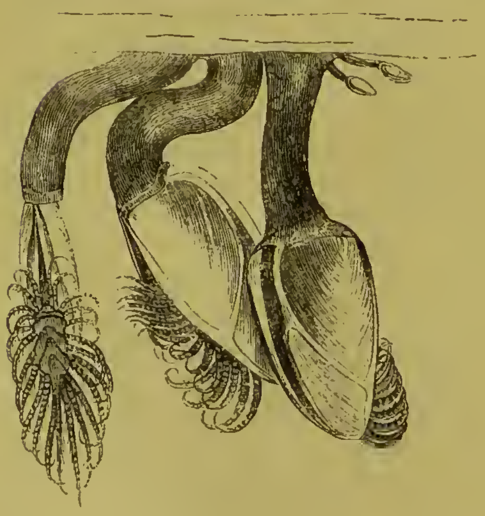
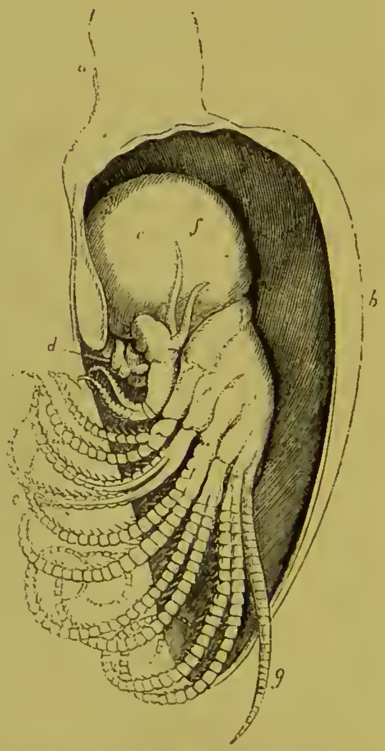


Fig. 5.



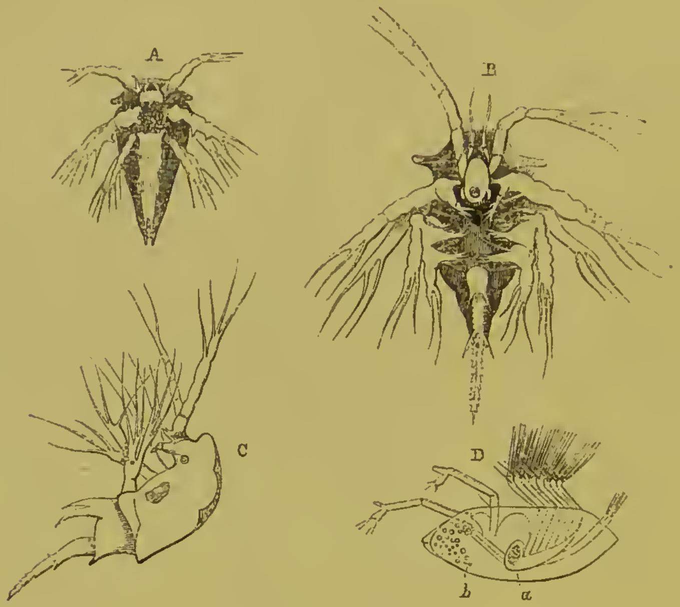
Anatifa lævis;—A, group of animals of different ages, as attached in the living state:—B, interior structure, enlarged, as shown by the removal of the valves of one side; *a*, peduncle; *b*, mantle; *c*, cephalic portion of the body; *d*, mouth; *e*, articulated members; *f*, flabelliform appendages (or branchiæ); *g*, abdominal appendage.

effected, in great measure, for the Vertebrated series. In the determination of the relative importance of characters, it is certain that great assistance may be expected from the study of development; although we may not perhaps go the full length with those who maintain, that it should constitute the sole basis of all classification (§ 76).—It would be scarcely possible to adduce a more apposite illustration of the essential importance of this knowledge, to the determination of the true position and relations of a group of Animals distinguished by characters that seem to isolate it from all others, than is afforded by the case of the *Cirrhipeds*, or Barnacle tribe (Fig. 4). By all the earlier Naturalists, this group was unhesitatingly referred to the Molluscous sub-kingdom; being allied to the classes of which that division is composed, in the softness of its body and appendages,—in the inclusion of these within a hard casing, that is not fitted upon them, like the 'test' of a Crab or Lobster, but loosely envelopes the whole, like the 'shell' of a Mussel or Limpet,—and in the fixity of the animal to one spot during (apparently) the whole of its existence, the *Barnacle* being anchored by a long flexible tubular peduncle, as a Pinna is anchored by its byssus, whilst the *Balanus* is attached, like the Oyster, by the adhesion of the shell itself to some solid basis of support. Even Cuvier left them in this position; although he had been led by the study of the anatomy of the animal inhabitants of the shells, to recognize their strong affinities to the Articulated series. For he perceived that their bodies are quite symmetrical, and present indications of division into a longitudinal succession of segments, each of them furnished (Fig. 5.) with a pair of articulated appendages; their mouth he observed to be furnished with lateral jaws; he found their heart to lie in the dorsal region; whilst along their ventral region he detected the double ganglionic nervous chain, so characteristic of Articulated animals. Those Naturalists who considered this last assemblage of characters to possess a higher value than the preceding,—as being more indicative of the *essential* nature of these animals, whilst their relations to the Molluscous series are rather such as *adapt* them to a particular mode of life,—transferred the Cirrhipeds to the Articulated series; and the propriety of this transference was made manifest by the discovery (first announced by Mr. J. V. Thompson in 1830*), that the Cirrhipeds in their early state are free-moving animals, conformable in all essential particulars to the *Crustacean* type; and that they only attain their adult form and character after a series of metamorphoses, which progressively remove them to a greater and greater distance from it, and which, while they constantly tend to evolve the peculiar conformation that distinguishes the Cirrhiped group, adapt the animal, in each of its stages, to maintain its own existence. The researches of Mr. Thompson, with the extensions which they have subsequently received from others, show that there is no essential difference between the early forms of the *sessile* and of the *pedunculated* Cirrhipeds; but that both are active little animals (Fig. 5, A), possessing three pairs of legs and a pair of compound eyes, and having the body covered with an expanded shield, like that of many Entomostracous Crustaceans, so as in no essential particular to differ from the larva of *Cyclops* (Fig. 60). After going through a series of metamorphoses, one

* "Zoological Researches," No. III.

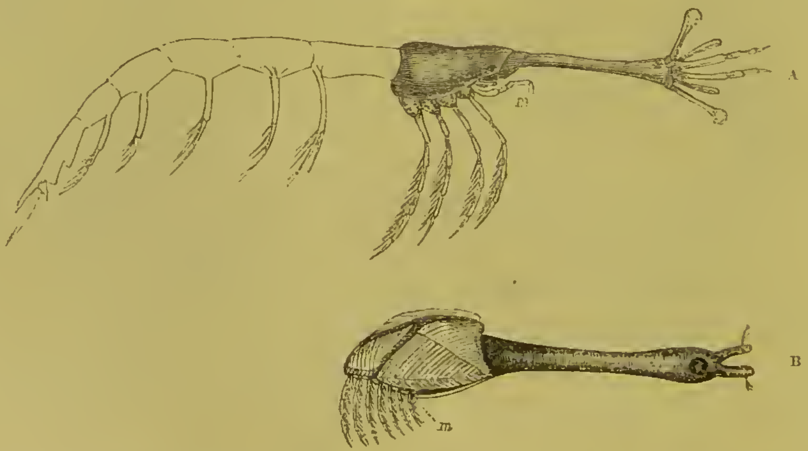
stage of which is represented in Fig. 6, B, these larvæ come to present a form D, which reminds us of that of *Daphnia*, another Entomostracous Crustacean; the body being enclosed in a shell, composed of two valves, which are united along the back, whilst they are free along their lower margin, where they separate for the protrusion of a large and strong anterior pair of prehensile limbs provided with an adhesive sucker and hooks, and of six pairs of posterior legs adapted for swimming. This bivalve shell, with the prehensile and natatory legs, is subsequently thrown off; the animal then attaches itself to its *head*, a portion of which

FIG. 6.



Development of *Balanus balanoides*;—A, earliest form;—B, larva after second moult;—C, side view of the same;—D, stage immediately preceding the loss of activity; *a*, stomach (?); *b*, nucleus of future attachment (?).

FIG. 7.



Comparison of *Leucifer*, a Stomapod Crustacean, with *Lepas*;—in the former, A, the abdomen, which becomes rudimentary in Cirrhipeds, is represented in outline;—in the latter, B, the antennæ and eyes, which really exist in the larva, are represented as if they had been retained and had continued to grow; *m* marks the position of the mouth in both.

becomes excessively elongated into the peduncle of the Barnacle (Fig. 7), whilst in the Balanus it expands into a broad base or disk of adhesion; the first thoracic segment sends backwards a prolongation which arches over the rest of the body so as completely to enclose it (no uncommon occurrence among the Crustacea), and the exterior layer of this is consolidated into the 'multivalve' shell; whilst from the other thoracic segments are evolved the six pairs of cirrhi which are characteristic of these animals in their adult state.—Hence, whether we consider the peculiarities of the group, in the fully-developed condition, as sufficient to entitle it to take rank as a distinct class, or whether we regard it as constituting merely a section of the great Crustacean class, there can be no longer any question that the Cirrhipeds bear any extremely close affinity to the latter, and that they must be placed near its borders (whether within or beyond them), as an aberrant form of the higher Articulate type, adapted to a life essentially Molluscous.*

15. Much of the controversy which has taken place among Physiologists, in regard to the general doctrines which may be deduced from the comparison of different plans of organisation, has been due to a neglect of this difference between *functional* and *structural* correspondence, that is, between *analogy* and *homology;* whereby phenomena which are essentially dissimilar, have been brought under the same category. But by some who have clearly recognized *organic identity* as the basis of their reasoning, it has been attempted to show that the law of *Unity of Composition* has an unlimited application; it having been maintained that the same elementary parts exist alike throughout the Vegetable and Animal Kingdoms, and that the difference between the several classes of each lies solely in the respective development of these parts. Such a doctrine, however, can only be supported by assertion, since Nature affords no sanction to it; as the most cursory survey of these two of her kingdoms will at once make obvious.

16. If, for example, we commence by comparing the various tribes of Flowering-Plants with each other, we find that they may all be referred to a certain 'archetype' or ideal form, consisting of an ascending axis or stem with its foliaceous and floral appendages, and of a descending axis or root with its absorbent fibres. Their most obvious diversities are generally attributable to the deficiency or excess of some or other of these component parts: thus many of the trees most remarkable for the massive perfection of their stems, have the less essential parts of their flowers undeveloped; whilst many of the plants most remarkable for the beauty and luxuriance of their blossoms, never form a true woody stem. But amid this general conformity, the Botanist recognizes two very distinct though subordinate types, each of them including a long series of gradational forms, from the lofty tree to the humble plant; the difference between which consists rather in the diversity of the *plan* on which the very same elementary parts are combined and arranged, than in any superior elevation possessed by one over the other. Thus if we compare the Palm and the Oak, which may be considered as presenting typical

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* For the most complete account of these metamorphoses, as well as of the Anatomy, Physiology, and Classification of the *pedunculated* division of the group, see Mr. C. Darwin's "Monograph on the sub-class Cirripedia," published by the Ray Society, 1851. —It is hoped that this admirable work will be soon completed, by a like description of the *sessile* division.

examples of the *Endogenous* and *Exogenous* stems, we find that the same materials—cellular tissue, woody fibre, and ducts of various kinds—are worked-up, as it were, on two different patterns; and as a like difference of plan extends itself also to the arrangement of the elementary parts of the leaf and to the number of the components of the flower, and even shows itself in almost the earliest stage of the life of the embryo, it becomes apparent that the diversity is one which belongs to the fundamental nature of the two groups. There are instances, it is true, in which there is such a general conformity in external appearance between certain of their members (between *Cycads* and *Palms* for example), as might deceive a mere superficial observer; yet there is no assumption of the essential characters of the latter of these groups by the former, the stem being exogenous and the embryo polycotyledonous. So, again, although there are certain Flowering-plants (such as *Lemna*, duckweed, and *Zostera*, sea-wrack) which, alike in habit and in general simplicity of structure, correspond with aquatic Cryptogamia, these are at once recognized as degraded forms of the Phanerogamic type, when their generative apparatus is examined; reduced, though this is, to a condition of extreme simplicity.—The Cryptogamic series cannot be referred with equal propriety to a single 'archetype,' so diversified are the types of structure, as well as of grades of development which its principal groups present. Still the plan on which their generative apparatus is constructed, though not so dissimilar to that of Phanerogamia as was formerly supposed (since no reasonable doubt can now remain of their true *sexuality*) present a certain fundamental uniformity; whilst its several modifications serve to distinguish the subordinate groups of Ferns, Mosses, Liverworts, &c. Although the Cryptogamia as a whole rank below Flowering-plants, yet no one can help recognizing in a Tree-Fern a far more elaborate structure than that of *Lemna* or *Zostera;* so that the essential distinction between the two series lies, not in *grade* of development, but in *type* of conformation. So among the Cryptogamia themselves, we find *parallel* series, such as those of *Algæ, Lichens*, and *Fungi*, through each of which a certain distinctive type is preserved, notwithstanding that between their several varieties of grade there is a close correspondence.—Hence we see that although, from the comparatively small number of distinct organs which the Plant possesses, and from the less complete separation even of these, there is not by any means the same scope for varieties in plan of organisation as we shall find in the Animal Kingdom, it is not the less certain that a considerable number of *distinct types of structure* exists, which cannot be reconciled to any other theory of fundamental unity, than that which refers them all to their common starting-point—the single cell.

17. Turning, now, to the Animal Kingdom, we find that even a slight general survey affords ground for the recognition of those *four very distinct plans of structure*, which Cuvier was the first to mark-out clearly,—namely, the Radiated, the Molluscous, the Articulated, and the Vertebrated; and these are found to be more and more clearly distinguishable from each other, the more profoundly we examine into the fundamental peculiarities of each, and the more fully we become acquainted with the history of its development. For by accurately studying and comparing the various modifications under which these respectively present them-

selves, we see that beneath the apparent *mixture* of characters which occasionally presents itself (as, for example, in the case of the Cirrhipeds, 14), there is an *essential* conformity to one type, and that the departure from the ordinary aspect is merely superficial, being such as *adapts* the animal or group of animals to a particular mode of existence. Now since modifications of a similar kind may take place in groups of animals belonging to different types, they may come to present very striking resemblances to each other in their *adaptive* characters (as is the case between Birds and Insects), although there is no conformity whatever in their general plan of structure. Taken as a whole, no animal belonging to any one of these types can be likened to any animal belonging to another; although comparisons may be legitimately made between their individual organs. Thus, as Von Baer justly observes, "metamorphose a Cephalopod as you will, there is no making a Fish out of it, save by building-up all the parts afresh;" yet in many portions of their organisation, Cephalopods are unquestionably intermediate between the lower Mollusks and the typical Fishes. Again, although the higher Cephalopods indubitably take a more elevated rank as Animals than the lowest Fishes, and in this respect might be considered as approximating more closely to Man, yet in the conformity of its organisation to the Vertebrated type, the lowest Fish bears far more resemblance to Man, than does the highest Cephalopod.—Moreover it is to be observed, that the general type of construction manifests itself not merely in the mode in which the organs are grouped together, but also in the conformation of the organs themselves. Thus we shall hereafter see, that whilst there is a remarkable correspondence between the condition of the Circulating apparatus in the two series of Articulated and Molluscous animals,—especially as regards the imperfection of its vascular system, and its communication with the visceral cavity,—there is a *type* which is peculiar to each, and which shows itself in the structure of the heart, as well as in the general distribution of the blood-vessels. For the type of the heart, in the Articulated animal, is the elongated dorsal vessel, which, if divided at all, has a repetition of similar chambers for the several segments of the body; whilst in the Mollusk it is a concentrated organ, with much thicker walls, usually having the auricle or receiving cavity separated from the ventricle or impelling cavity, and presenting no other repetition of similar parts than the occasional doubling of the auricle, where the two sets of gills (whence the blood returns to the heart) are placed wide asunder. So, again, in the various Glandular organs of the Articulata, the required extent of surface is usually afforded by the elongation of a small number of narrow tubes; whilst in the Mollusca, the same extension is provided for by the multiplication of short and wide follicles. Yet we find that in certain Crustacea, which are adapted in many respects to the conditions of the Mollusk, both the heart and the glandular apparatus present a very striking approximation to the Molluscous type; whilst no such approximation is seen in the general plan of the fabric, which is as obviously articulated in the Crustacea, as it is in the Insect.

18. But although it is in *type*, or plan of organisation, that the most essential differences lie, among the several forms of Plants and Animals, it is not the less true that they are distinguished by very marked diversities in *grade of development;* by which is to be understood, the degree in

which the several parts that make up the entire fabric are characterised by specialities of conformation, so that each becomes a distinct *organ*, adapted to perform a *function* more or less different from that which other parts can discharge. The lower we descend in the scale of being, whether in the Animal or in the Vegetable series, the nearer approach do we make to that *homogeneousness* which is the typical attribute of inorganic bodies, wherein every particle has all the characters of individuality, so that there is no distinction either of tissues or of organs. Thus in Sponges and Sea-weeds, even when of considerable size, every part resembles other parts in intimate structure, and differs but slightly from them even in external configuration; so that the whole mass is little else than a repetition of the same organic components. On the other hand, as we ascend the scale of being, we find the fabric—whether of the Plant or the Animal—becoming more and more *heterogeneous;* that is, to use Von Baer's language, "a differentiation of the body into organic systems, and of these again into separate more individualized sections," presents itself. Thus, as we ascend from the lowest towards the highest forms of Vegetable life, we find that out of the homogeneous aggregation of cells which forms the simple frond of the humble Algæ (§ 22), a *differentiation* gradually arises between the 'axis' and the 'appendages to the axis;' that in the axis, there is a gradual separation established between the ascending portion, or stem, and the descending portion, or root; and that among its appendages, the foliaceous organs become more and more completely separated from the generative apparatus. Even in the highest Plants, however, we find an extensive *repetition of similar parts;* and there is always, too, a close correspondence in the intimate structure of even the most antagonistic organs, such as the roots and leaves.—The differentiation, both as regards external conformation and intimate structure, proceeds to a far wider extent in the Animal kingdom, in virtue of the much greater variety of purposes to be attained in its existence; and we see this carried to its highest degree in Man, in whose organism the principle of *specialisation* everywhere manifests itself, no part being a precise repetition of any other, except of the corresponding part on the opposite side of the body.*

19. It is only, however, by a very gradual succession of steps, that this elevation is attained. The simplest Animals are precisely upon a level with the simplest Plants, as regards their homogeneity of character; and no sooner does a differentiation of organs show itself, than these are in the first instance almost indefinitely repeated, so that, however numerous may be the parts of which the entire organism is composed, they are (so to speak) the *fac-similes* of one another. Thus not only in Zoophytes, but also in the lower Mollusca and Articulata, we find this repetition extending to those entire *groups of organs,* which, when detached from the rest, can maintain an independent existence, and are therefore commonly accounted distinct individuals. But we find the same to hold good, as

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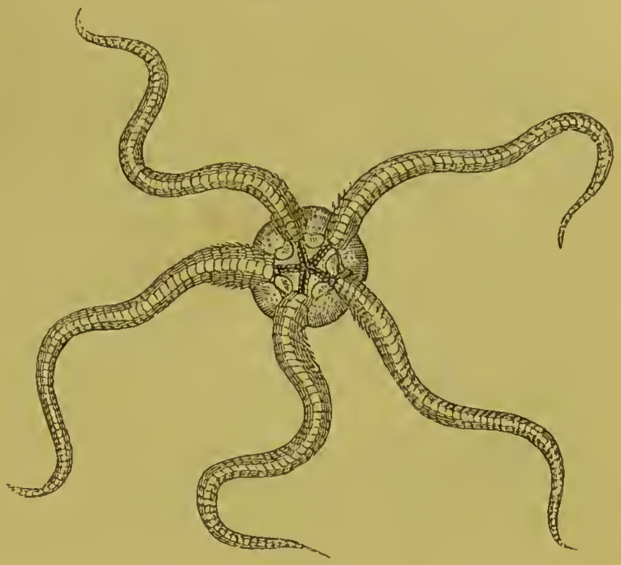
* This fact is most curiously exemplified in the speciality of the *seats of election* of those disorders of nutrition, which obviously depend upon the presence of a *materies morbi* in the blood, rather than upon any primary local disturbance.—See Dr. William Budd's Memoir on "Symmetrical Diseases," in the "Medico-Chirurgical Transactions," Vol. XXV.; Mr. Paget's "Lectures on Surgical Pathology," Vol. I. p. 17 *et seq.*, and the Author's "Principles of Human Physiology," 4th Ed., p. 192.

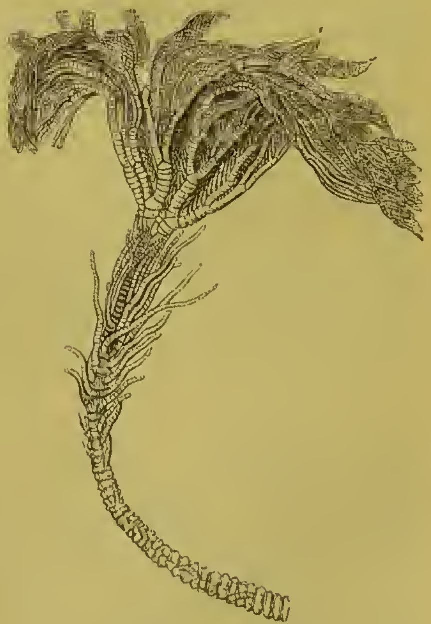
regards *individual organs*, in the highest members of each of the Invertebrated sub-kingdoms, and even (though to a less extent) among Vertebrated animals. Thus among the *Echinodermata*, there is a precise repetition of similar parts around a common centre; and although this repetition is limited to *five* in the highest forms of the class, yet it extends to a much greater number in those of inferior organisation,—as we see in comparing the *Ophiura* with its five simple arms (Fig. 8) and the *Pentacrinus* (Fig. 9), whose ten arms all subdivide into such numerous branches, that the aggregate number of pieces in the whole is estimated at above a hundred thousand. So, again, in the *Cephalopoda*, which constitute the highest division of the Molluscous series, we find the tentacula surrounding the mouth to be almost indefinitely multiplied in the lower or *tetrabranchiate* division (*Nautilus* and its allies); whilst they are reduced to eight or ten in the *dibranchiate* order (*Cuttle-fish*, Fig. 47), at the same time acquiring a much higher individual development, and often having one pair differentiated from the rest, for some special purpose. So in the *Annelida* and other inferior groups of the Articulate series, we find the locomotive, respiratory, and other important organs almost indefinitely multiplied in the longitudinally-repeated segments; but as we ascend towards the higher Articulata, the number of segments becomes strictly limited and greatly reduced, even where these divisions are still little else than repetitions of one another,—being only twenty-two in the Centipede, and thirteen in the Insect-Larva; whilst in the perfect Insect, the differentiation is carried to its highest extent, the locomotive apparatus being restricted to the three thoracic segments, and all the other organs, even when repeated throughout, being unequally developed in the several parts. The same principle of gradual differentiation

FIG. 8.



Ophiura.

FIG. 9.



Pentacrinites briareus.

shows itself most remarkably in the conformation of the members of Vertebrata: for, taking the many-jointed but single rod-like appendage of the *Lepidosiren* (Fig. 3, A, and Fig. 150) as their lowest type, we find this simply repeated even to the extent of a hundred-fold or more, in the digital rays supporting each of the pectoral and ventral fins of *Fishes;* as we ascend thence, through the extinct *Enaliosauria* (Ichthyosaurus, Plesiosaurus, &c.) to the typical Reptiles, we find the number of these multiplied digits diminishing, until it settles down at five, and the number of joints in each also reduced, until it becomes restricted to the six rows (two carpal, one metacarpal, and three phalangeal) which characterise the hand (or foot) of Man; in *Birds* and *Flying Mammals* there is a most marked differentiation between the anterior and posterior extremities, as there is also (though in a less degree) in Man; and in the *Quadrumana,* we begin to see that specialisation of the first digit (this being usually common to all *their* members) which is carried to its highest point in the hand of *Man,* whose other digits, also, have their distinctive capabilities, whereby this member as a whole becomes the most highly-organised of all instruments, in virtue of the unequalled variety of actions which it is adapted to perform.

20. Thus we see that, whether we trace the 'Archetype' of each great subdivision of the Animal kingdom into those modifications which it presents in the more restricted groups,—or whether we follow any organ or system, from the form under which it at first presents itself, to that which it assumes in its state of most complete development,—we recognise one and the same plan of progression, namely, *from the general to the special;* and, as Von Baer justly remarks, the relations of any organised fabric to any other, must be expressed by the product of its *type* with its *grade of development.* Neither alone suffices to characterise it; for under the same type, different grades of development may present themselves; whilst conversely, a like grade of development may be attained under different types. And this general fact needs to be constantly borne in mind, not merely when a Plant or Animal is being considered as a whole, but also when we are studying the evolution of any individual organ or system in the ascending series; since it is no more possible to follow this through one unbroken progression, than it is to arrange the entire assemblage of beings composing either kingdom in a single linear series.—It may in some degree assist the reader in his perusal of the subsequent pages, if we here pause to take a general survey of the principal types of Vegetable and Animal conformation, and of the chief diversities in grade of development which present themselves under each.

21. *Vegetable Kingdom.*—If we commence by examining any Plant of high organization, we observe, in the first place, that there is a complete differentiation between its organs of *Nutrition* and its organs of *Reproduction;* and further, that its principal organs of Nutrition, the *root* and the *leaf,* are separated from each other by the interposition of the *stem* or *axis,* around which the various appendages are arranged with a considerable degree of regularity. Further, we notice that a corresponding differentiation presents itself, as to the *intimate structure* of these several organs; for whilst the parts most directly concerned in the vital opera-

tions of the organism are chiefly made-up of aggregations of *cells*, which resemble in all essential particulars those of which the simpler forms of vegetation entirely consist, these are supported upon a framework of *woody fibre*, an extension of that which gives strength and solidity to the stem and roots; and further, in order that air and liquids may the more readily find their way from one part of the structure to another, than they could do by transmission from cell to cell, a set of *ducts* is interposed, which establish a ready communication through the stem between the roots and the leaves. These organs are all mutually dependent and connected; and contribute, each in its own special manner, to the life of the Plant *as a whole.* But since all the most essential organs are many times repeated, the loss of some of these does not involve the destruction of the entire organism; and even the separated parts may develope the organs in which they are deficient, and may thus evolve themselves into entire plants, and maintain an independent existence.* In this way a *multiplication* of the products of the original germ may be effected; but these, as will be shown hereafter (CHAP. XI.), are not distinct *individuals* in the highest sense of that term; and the process by which they are evolved is simply a modification of the ordinary Nutritive operation, and is so far from being a form of true Generation, as to be essentially antagonistic to it. This distinction is one of much importance; since on it depends the recognition of the organs in Cryptogamia, which are homologous with those of Flowering-Plants.

22. Having thus determined, by the analysis of one of the highest Plants, what it is that constitutes the *most complete* type of Vegetable organisation, we shall commence with the lowest division of the series, and endeavour to trace-out the principal lines of ascent by which that type is attained. This can only be accomplished, at present, in a very imperfect manner; since it is only within a very recent period, that the homologies of the reproductive apparatus of Phanerogamia have been discovered among Cryptogamia; and little more than a guess can be as yet made, as to the conditions which these present in some of the humbler forms of Cryptogamic life.—The lowest type of vegetable existence is afforded by those organisms, which either consist of *single cells*, or of *aggregations of similar cells*, each of which can maintain an independent existence, living *for* and *by* itself, and not needing the co-operation of other cells, save for the purpose of generation, of which the re-union of the contents of two cells, by an act of 'conjugation,' is an essential condition. Any one of these cells may *multiply* itself indefinitely by subdivision, the results of which process are seen in the accompanying example (Fig. 10); but these products are all mere *repetitions* one of another, and often detach themselves spontaneously, so that the descendants of a single cell may cover a very extended area, as is the case, for example,

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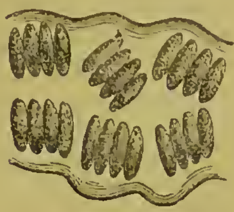
* This is usually the case under favourable conditions with regard to *leaf-buds*, which can put forth rootlets, and then evolve a stem, from which other leaf-buds and their flower-buds are developed. But there are some plants, as *Bryophyllum*, which have the same power in every *leaf*, or even in every *fragment* of a leaf; a small portion, laid upon damp earth, or suspended in a humid atmosphere, gradually evolving itself into the entire organ, and at the same time developing the other parts most essential to the performance of its nutritive operations, from which the reproductive apparatus is subsequently put forth.

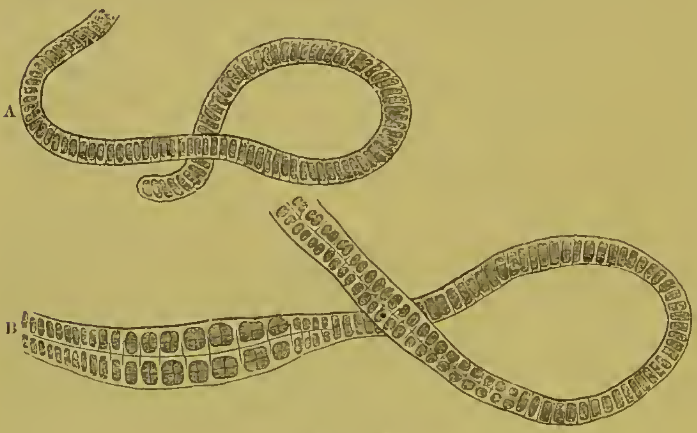
with the *Protococcus nivalis*, or 'red snow.' There is here, therefore, not the least show of differentiation; no special cells being set apart even for the performance of the generative act. Where the multiplied cells remain in continuous connexion with each other, being imbedded in a common substratum of gelatinous substance, so as to form but a single mass (Fig. 10), this may be perfectly homogeneous throughout; no definite form being presented by it as a whole, and no trace of 'organs' being distinguishable in any part of it. The first indication of progress towards a higher grade, is given by the limitation of the *direction* in which the increase takes place: so that, instead of an amorphous aggregation of cells, we find a linear series (Fig. 11, A) which is formed by successive transverse subdivision; and this filament may increase in breadth by longitudinal subdivision (B), so as at last to produce a laminar expansion, such as that of the common *Ulvæ*, which is termed a *thallus*. In the simplest forms of this thallus, we do not meet with the slightest trace of differentiation; and every one of its component cells appears to live as much for and by itself, as if it were completely detached from the rest. Every one of them, moreover, seems able to multiply itself, not merely by subdivision, but also by the emission of a portion of its contents enclosed in a cell-wall, in the condition of a 'spore' or detached *gemma;* and this in the tribe now under consideration, being usually furnished with cilia, and endowed with the power of spontaneously moving for a time, is termed a 'zoospore.' When the zoospore has been thus carried to a distance from the organism from which it proceeded, it begins to develope itself into a similar organism by the process of duplicative subdivision; and in arriving at the highest of these stages of development, it passes through the simpler forms which remain permanent in yet humbler grades of vegetation. The true Generation of the plants of this group, to which the term *Protophytes* may perhaps be advantageously restricted, seems to be always accomplished by the process of 'conjugation,' in which any or all of the component cells may alike participate; but we see, in its higher forms, a tendency to the distinction between the 'sperm-cell' and the 'germ-cell,' that is, to the differentiation of sexes into male and female,—the only mark of heterogeneousness which yet presents itself. The product of this act is a new cell, from which a new plant originates

FIG. 10.



Hormospora transversalis.

FIG. 11.



Bangia velutina.

by duplicative subdivision, as in the case of the zoospore. Here, then, we find that each individual (understanding by this term the aggregate result of a generative act) is made up of an indefinite number of cells, which, being precisely similar to each other, have no relation of mutual dependence; so that the Life of the whole is merely the *sum* of the lives of the component parts, and not, as in higher organisms, the *product* of it.

23. In the next stage of development, the differentiation of parts begins to manifest itself more decidedly; but this not so much in a distinction of organs adapted to separate offices in the act of Nutrition, as in the limitation of the Reproductive act to particular portions of the organism, and in the setting-apart of special organs for its performance. For we have as yet no real distinction between stem, roots, and leaves; although some semblance of such a distinction may present itself. The primordial cell, by repeated subdivision, extends itself into a 'thallus,' whose form has but little definiteness, and whose tissue is nearly homogeneous throughout, being entirely composed of cells of various forms, without either woody fibres or vessels of any kind; and it is chiefly by its apparatus of fructification, which presents itself under many different aspects, that this group, which may be designated by the term THALLOGENS, is distinguished from the preceding. Nearly the same degree of general development is presented by three tribes of these humble Cryptogamia, —namely, *Algæ*,* *Lichens*, and *Fungi*,—which, nevertheless, are fitted to exist under very diverse conditions, and which present corresponding diversities of structural type; and all of them seem to agree (according to the most recent investigations, of which an account will be given hereafter, CHAP. XI.) in the possession of a special generative apparatus, in which the distinction of sexes is clearly marked. This consists of a set of 'sperm-cells' developed in certain parts of the organism, and of a set of 'germ-cells' evolved elsewhere, usually (but not always) in the same individual; the product of the former is a 'spermatoid' body, which comes into contact with the latter and fertilizes its contents; and the result is the formation of a germ, which must be considered as the commencement of a new generation. This germ, however, frequently remains for some time in connection with the parent, and multiplies itself by duplicative subdivision at the expense of the nutriment which it draws from it, so as at last to evolve itself into a collection of 'spores' contained within a special envelope, every one of which, when liberated from the parent, may develope itself into a new plant in which the same processes are repeated. It is by the general relation of this apparatus of fructification to that of nutrition, that the three groups already named are most distinctively characterized.

24. Thus the *Algæ* vegetate exclusively in water or in damp situations; they require no nutriment but such as is supplied by water and by the air and inorganic substances dissolved in it; they absorb this nutriment equally by every part of their surface; and they show a great tendency to the extension of the 'thallus' by the multiplication of cells in continuity with the existing fabric, so that it frequently attains most

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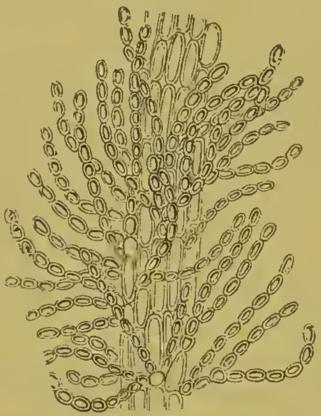
* The group of Algæ, as here limited, does not include the Protophytes described in the preceding paragraph; for although these, being mostly aquatic plants, are usually ranked in it, yet their type of reproductive apparatus is so distinct from that of the higher Algæ, as to require that they should be separately considered.

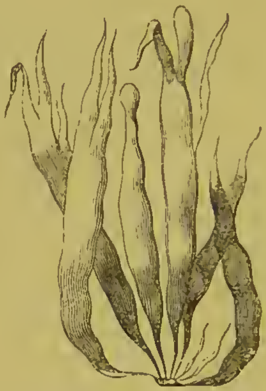
extraordinary dimensions. In some of the simpler forms of the group, we find but a slight advance upon those aggregations of similarly-shaped cells, of which the fabrics of the Protophyta are made up. Thus in *Mesogloia* (Fig. 12), although we have a distinct axis with radiating appendages, the former is composed of elongated cells very loosely adherent, while the latter consist of single rows, bearing the generative cells at their extremities; and in *Zonaria* (Fig. 13), it is only the character of the fructification that raises it above the type of an Ulva. In the highest Algæ, however, we find some differentiation in the texture of their interior and exterior substance; and there is also a certain foreshadowing of the separation between the stem, the roots, and the leafy expansion or frond; but there is nowhere a departure from the simple cellular type, nor is there any real specialization of function, save that the fructification

Fig. 12.



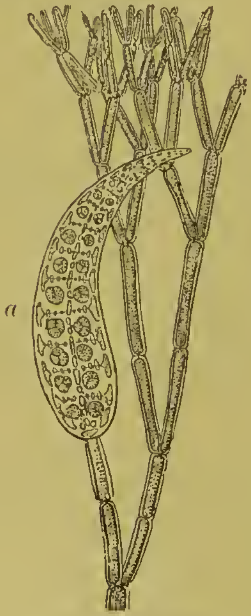
Mesogloia vermicularis.

Fig. 13.



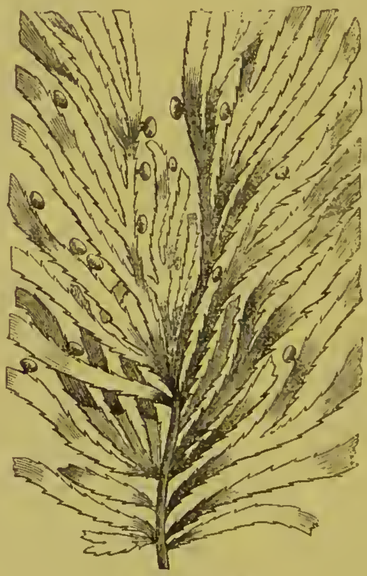
Zonaria plantaginea.

Fig. 14.



Dasya kuetzingiana.

Fig. 15.

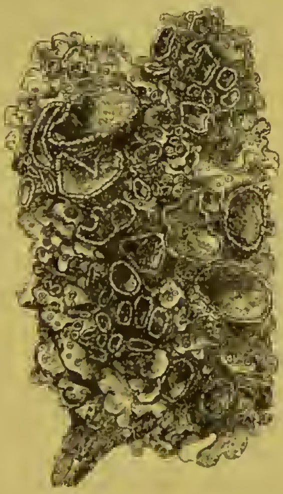


Marginaria gigas.

is evolved from the frondose portion, and not from the stem-like or root-like axis. Most Algæ are provided with a special apparatus (such as the *stichidium* of *Dasya*, Fig. 14, *a*) for the evolution of free gemmæ, which are sometimes ciliated like the zoospores of Protophyta, and which multiply the original fabric independently of any true generative act. The proper generative organs are frequently very obscure, and are often buried in the general substance of the frond; occasionally, however, they form conceptacles, which are prominent externally (Fig. 15), or are developed on particular branches only. The embryo-cells, which are the products of the fertilization of the germ-cells by the contents of the sperm-cells, do not usually undergo any great amount of subdivision into 'spores,'* before each spore that has originated from it begins to develope itself into a new plant. Hence it is obvious that the whole *nisus* of vital activity in the Algæ, is towards Nutrition rather than Generation,—the multiplication of independent organisms of the existing generation, rather than the origination of new series by the proper generative act.

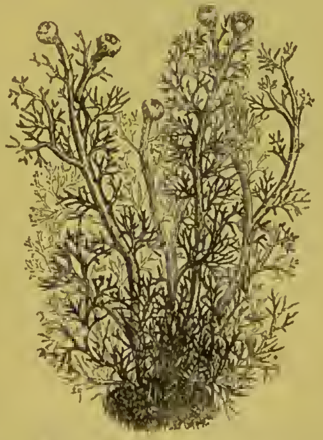
25. On the other hand, *Lichens* grow upon living Plants, upon rocks and stones, upon hard earth, or other situations in which they are sparingly supplied with moisture, but are freely exposed to light and air. They derive their food from the atmosphere, and from the water which this conveys to them; but this they do not seem to absorb equally over the whole surface, the least exposed side being the softer, and being probably the one through which most liquid is imbibed, whilst it is rather through the other that carbon is drawn-in from the air. The 'nisus' or tendency of development is here to form a hard crust-like thallus, of slow growth, and of rather limited dimensions, but of great durability (Figs. 16, 17); and in the several layers of this thallus, there is consi-

Fig. 16.



Parmelia acetabulum.

Fig. 17.



Sphærophoron coralloides.

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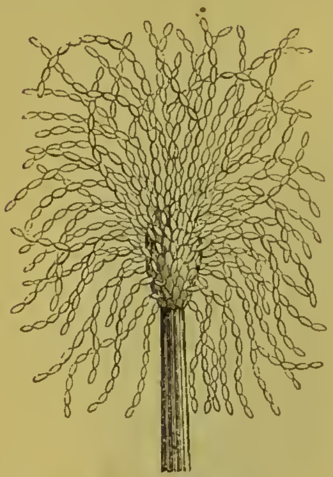
* The term 'spore' has been used to designate many things homologically different. The Author believes that it will be most accordant with existing usage, to continue to apply it to the bodies contained in the capsules of Mosses, Ferns, &c., which are immediate or remote products of the subdivision of the embryo-cell, and to those bodies in Algæ, Lichens, &c., which are homologous with them. On the other hand, the germ-cells which themselves take part in the generative act, and from which the embryo-cells originate, should never be designated by the term spore.

derable diversity of texture, although (as in the Algæ) there is no departure from the simple cellular type. As in the Algæ, moreover, we usually find a special arrangement for the production of free gemmæ (*soredia*), by which the number of independent organisms of the same generation may be multiplied; and the evolution of these has been frequently considered as the true reproductive process. It is now almost certain, however, that in this ill-understood group, both 'sperm-cells' and 'germ-cells' exist, although usually buried in the substance of the thallus; and that of the clusters of 'spores' which make their appearance within special conceptacles, each, as in the Algæ, is the result of the subdivision (to a limited extent) of a single embryo-cell produced by the generative act. These conceptacles are sometimes buried in the substance of the thallus, although their presence usually makes itself known by the prominence which it causes (Figs. 16, 17). Some tribes of Lichens very closely approximate to Algæ, both in their conditions of growth, and in their general character; whilst others present an equally close approximation to Fungi; so that, as some botanists have ranked this group with the former, and others with the latter, it seems reasonable to regard it as an intermediate section, the types of which are equally far removed from both.

26. The group of *Fungi* differs from both the preceding, in requiring as the most favourable, if not as the absolute condition, for the development of the Plants belonging to it, the presence of dead or decaying organic matter, which shall afford by its decomposition a larger supply of carbonic acid and ammonia than the atmosphere and its moisture would alone furnish; their growth is favoured by darkness rather than by light; and, like higher plants when not acted-on by light, they absorb oxygen and set-free carbonic acid. Their simpler forms (Fig. 18) strongly remind us of the lower Algæ (compare Fig. 12) in their grade of development, the nutritive and reproductive portions not being differentiated; but in the higher we find a very marked separation between these, the reproductive apparatus being here as predominant, as is the nutritive apparatus in the Algæ. The vegetative thallus of these plants, which extends itself indefinitely in situations favourable to its development, has a very loose flocculent texture, and is composed of elongated branching cells interlacing amongst each other, but having no intimate connection (Fig. 19, *a*); and this *mycelium*, as it is termed, has such a want of definiteness of form, and varies so little in the different tribes of Fungi, that no determination of species, genus, or even family, could be certainly made from it alone. Although any portion of this mycelium will continue to vegetate when separated from the rest, it does not appear that there is any provision for the spontaneous detachment of free *gemmæ* for the multiplication of the individual. The whole nisus of vital activity in the Fungi seems to be concentrated upon the Generative apparatus,

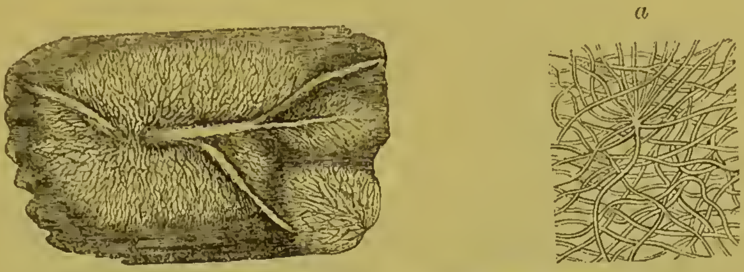
FIG. 18.



Stysanus caput-medusæ.

which, when fully developed, separates itself completely from the nutritive, and constitutes all that commonly attracts notice as *the Plant*

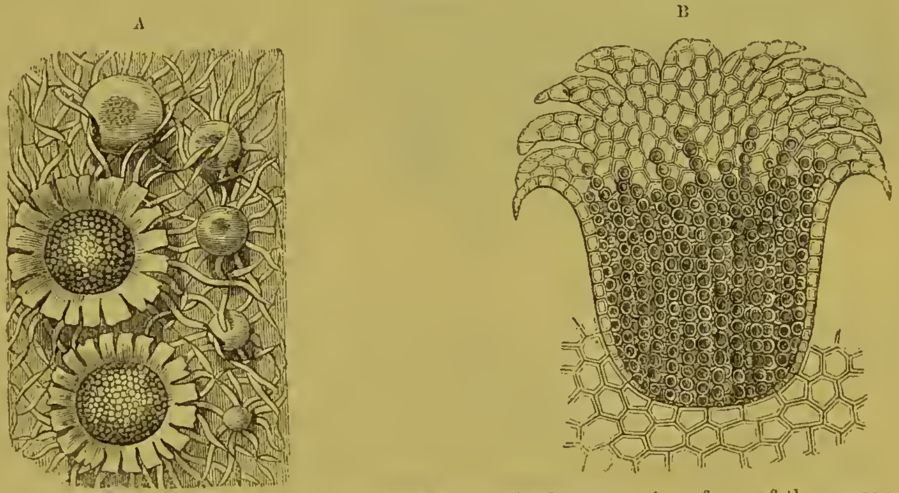
FIG. 19.



Clavaria crispula;—*a*, portion of the mycelium magnified.

(Fig. 20). Late observations render it probable that Fungi possess a true sexual apparatus, certain cells of the mycelium being developed into sperm-cells, and others into germ-cells; and that what is known as the 'fructification' is the product of an act of conjugation, the immediate result of which is the formation of an embryo-cell, which afterwards subdivides almost indefinitely, so as to produce an immense mass of 'spores.' These become detached from each other; and, being usually of extreme minuteness, are carried about in the atmosphere, so as to become deposited in remote soils, and to give rise to vast numbers of separate beings constituting a new generation.*

FIG. 20.



Æcidium tussilaginis:—A, portion of the plant magnified:—B, section of one of the conceptacles with its sporecles.

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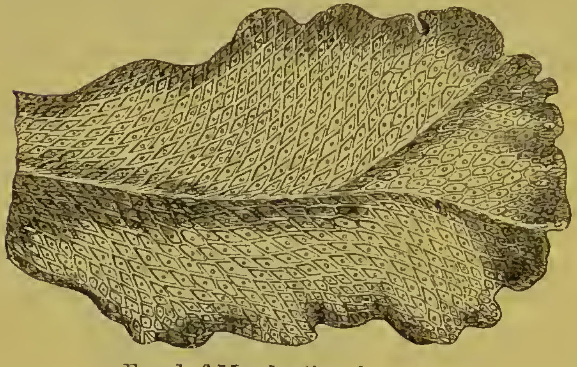
* It is interesting to observe that the mode of evolution of many of these Thallogens is greatly influenced by the conditions under which it takes place. Thus, if Lichens be removed from the influence of light, and be over-supplied with moisture, they show a tendency to the extension of the vegetative or foliaceous portion of the thallus, with a non-development of the fructification; and the thallus often assumes the *byssoid* form of the mycelium of Fungi, so that it might be readily mistaken for this. So, again, if the simpler forms of Fungi develope themselves in liquids, they show an unusual tendency to the extension of the mycelium; and may even take-on so much of the characteristic appearance and mode of growth of Algæ, that their true nature becomes apparent only when the fructification is evolved.—See the description of 'a Confervoid state of *Mucor clavatus*,' by the Rev. M. J. Berkeley, in the "Magazine of Zoology and Botany," Vol. II. p. 340.

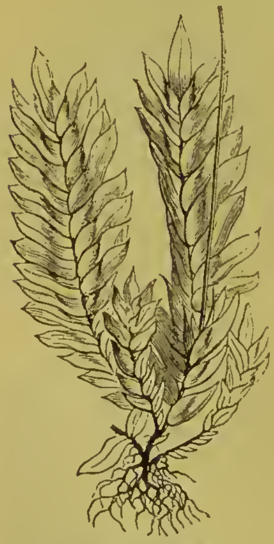
27. The next important mode of elevation consists in the differentiation of the parts of the Nutritive apparatus, and in their still more complete separation from the Generative. In ascending through the series formed by *Hepaticæ*, *Mosses*, and *Ferns*, we observe a progressive approximation to that distinction between the 'axis' and its 'appendages,' which is characteristic of the highest forms of Vegetable life; but the growth of the axis is limited to one or both of its extremities, the part already formed being subject to very little, if any, increase; and from this character it has been proposed (by Dr. Lindley) to distinguish this higher division of the Cryptogamic series by the title ACROGENS, significant of growth at their points alone.—The lower forms of the *Hepaticæ* (such as the *Ricciaceæ*) closely abut upon the Lichens, and differ from them but little as regards the organisation of their nutritive apparatus, although their fructification evolves itself after a different type. In the common *Marchantia* (Fig. 21), however, the soft green thallus now assumes more of the structure and aspect of a leaf, having an upper and under cuticle (the former perforated with stomata), and an intervening soft, loose parenchyma; and distinct radical fibres are thrown out from the lower surface, for the imbibition of moisture. In the *Jungermannia* there is a distinct axis of growth, on which the foliaceous appendages are symmetrically arranged; these are not completely differentiated from it in some species, but in others they are quite separated, and have an indication of a central mid-rib; the stem, however, still trails on the ground, and radical fibres are developed from every part of it.—A slight elevation in this type brings us to that of the *Mosses*, which always have a distinct axis of growth, commonly more or less erect, with the foliaceous appendages symmetrically arranged upon it (Fig. 22). A transverse section of this axis shows an indication of a separation between its *cortical* and its *medullary* portions, by the intervention of a layer of elongated cells, that seems to prefigure the *wood* of higher plants; and from this layer, prolongations pass into the leaves, in which they form a kind of mid-rib. The leaves, however, do not themselves present any considerable advance towards the more perfect type, being merely solid homogeneous aggregations of cells. And no proper root is yet evolved as a descending continuation of the axis, radical-fibres being put forth from every part of

FIG. 21.



Frond of *Marchantia polymorpha.*

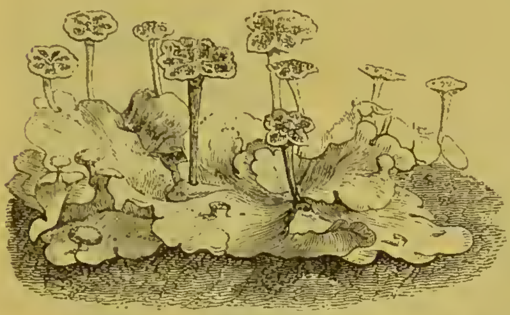
FIG. 22.



Fissidens bryoides.

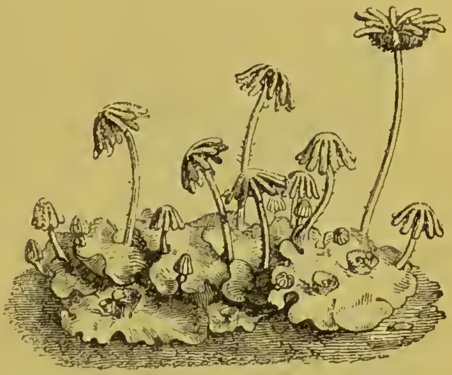
the lower portion of the axis (Fig. 25), and even from the under-surfaces of the leaves. Both in Hepaticæ and Mosses, we find a special arrangement for the multiplication of the plant by the formation of detached *gemmæ;* and

Fig. 23.



Marchantia polymorpha, with peltate receptacles bearing antheridia.

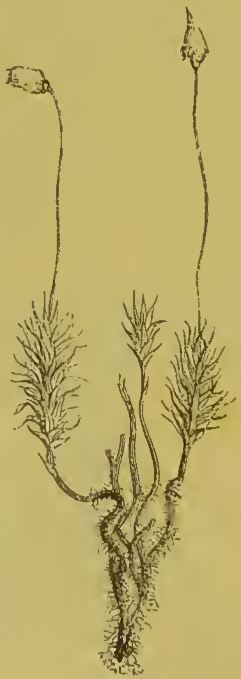
Fig. 24.



Marchantia polymorpha, with lobed receptacles bearing pistillidia.

some species owe their dispersion and perpetuation much more to this mode of propagation, than to the regular generative operation. There is no longer any doubt that both these tribes of plants possess true sexual organs; namely, *antheridia* containing 'sperm-cells,' and *pistillidia* or *archegonia* containing 'germ-cells.' In *Marchantia*, these are borne upon distinct plants, and both are sufficiently conspicuous (Figs. 23, 24); in Mosses, on the other hand, they are usually very obscure, and are generally combined in the same individual. The product of the fertilization of one of the germ-cells by the spermatoid bodies set free from the sperm-cells, is an embryo-cell which develops itself into a *capsule* containing a mass of 'spores;' and this, in the Mosses, is raised by the elongation of its footstalk, far above the original situation of the pistillidium, and becomes the only ostensible fructification of the plant (Fig. 25). In any one of the spores thus formed by the duplicative subdivision of the embryo-cell, a new plant may originate.—It is chiefly by specialities in the structure of their generative apparatus, that the preceding groups are distinguished from each other; each having its own peculiar type of fructification, whilst presenting (as we have just seen) a tolerably regular gradation in the development of the organs of nutrition.

Fig. 25.

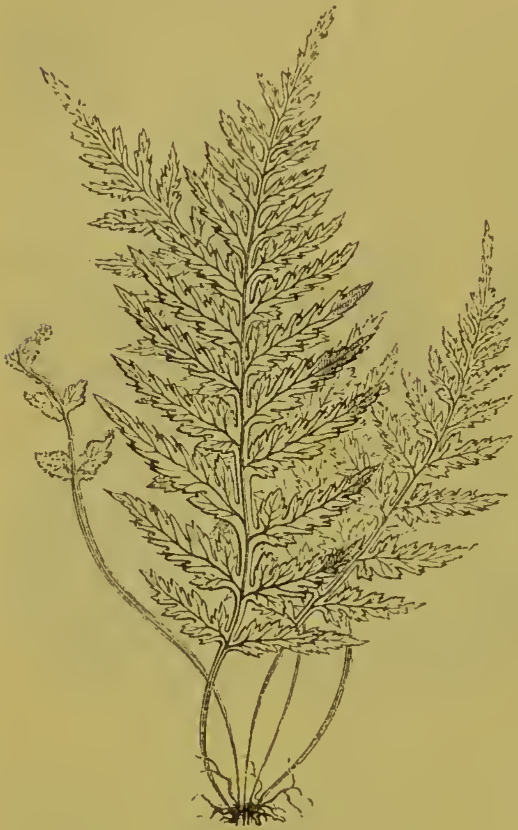


Polytrichum commune.

28. Passing from these to the *Ferns,* we find such a rapid elevation in the character of the apparatus of nutrition, as causes the group to approximate closely in this respect to the Phanerogamic division; indeed its members may be said to be more highly organized in most respects than the inferior Phanerogamia, although, the type of their generative apparatus being essentially Cryptogamic, they must be considered as

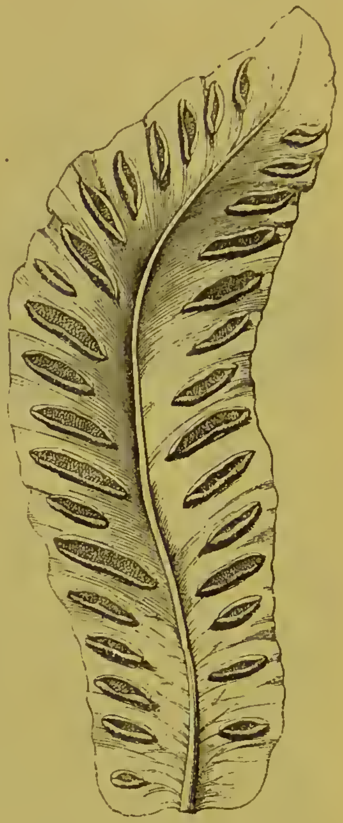
belonging to the lower rank in the Vegetable scale. It is in the Tree-Ferns that we have the most perfect evolution of the characters of the group; and here we find, not only an ascending axis or stem, around which the foliaceous appendages are symmetrically arranged in a spiral,

Fig. 26.



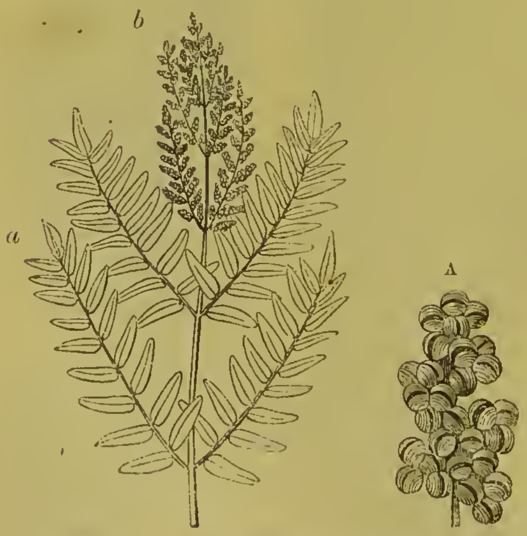
Trichomanes.

Fig. 27.



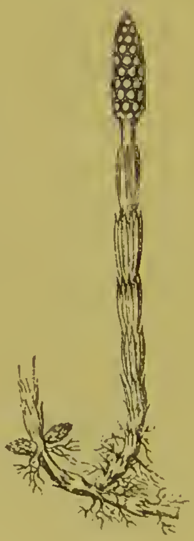
Frond of *Scolopendrum.*

Fig. 28.



Frond of *Osmunda regalis*;—*a*, sterile or foliaceous portion; *b*, fertile portion:—A, part of the latter enlarged, to show the thecæ.

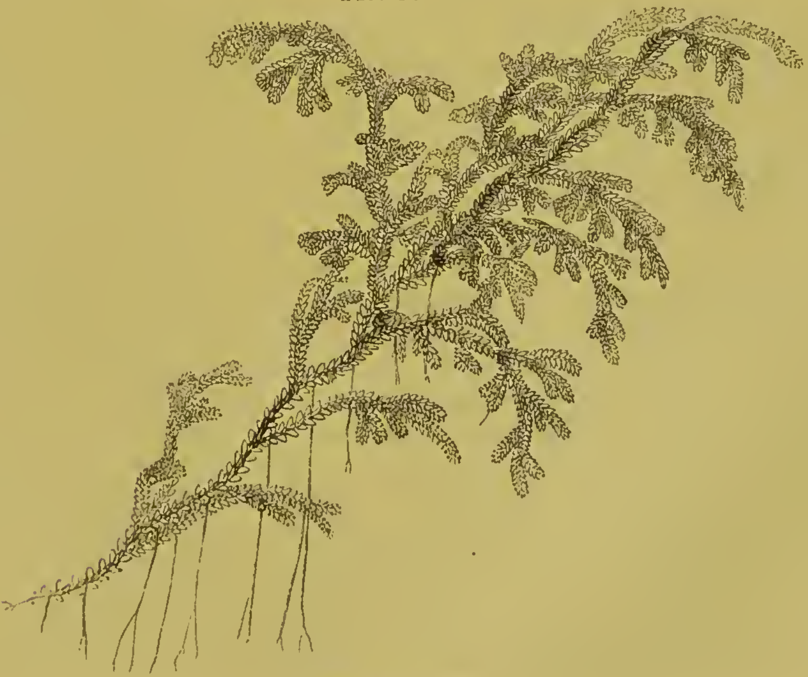
Fig. 29.



Equisetum arvense.

but a proper descending axis or true root, from which alone the radical fibres are given off. In the stem, the cortical portion is separated from the medullary by the interposition of bundles composed of woody fibre and vascular tissue; and the principal difference which exists between these and the woody layers of Exogenous stems, lies in the absence of any tendency to regular increase, except in length. From the fibro-vascular bundles in the stem, prolongations are given off, which pass into the leaf-stalks, and thence into the mid-rib and lateral branches of the foliaceous appendages, to which they form a kind of skeleton, as in the leaves of Phanerogamia. These organs, which are distinguished as 'fronds,' on account of their combining the character of a leaf with that of an apparatus of fructification, are constructed upon the same type with the leaves of Flowering-Plants; being composed of a cellular parenchyma, enclosed between two layers of epidermis, and having air-chambers to which access is given by stomata; and they can scarcely be less complete as organs of nutrition, although still made to bear a share in the function of reproduction. Even in this respect, however, a differentiation exhibits itself in certain Ferns, as the *Osmunda regalis* (Fig. 28); whose fructification is restricted to particular fronds, or parts of fronds, hence designated 'fertile,' which lose their foliaceous character; whilst the remainder bear no fructification, and are hence designated as 'sterile,' performing the functions of leaves alone. The ostensible organs of fructification are far from constituting (as they were until lately supposed to do) the real generative apparatus; for this is evolved at a period in the life of the plant, at which its appearance was totally unexpected. Each of the 'spore-cells' which are set free from conceptacles on the under surface of the fronds (Fig. 27), when received upon a damp soil, extends itself, by duplicative subdivision, into a frondose body closely resembling the thallus of the Marchantia; it is in this that the 'sperm-

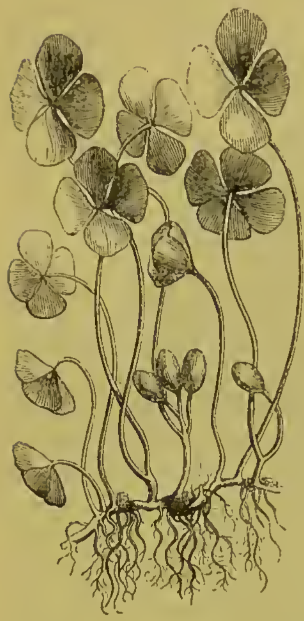
FIG. 30.



Lycopodium cernuum.

cells' and 'germ-cells' are evolved, and that the fertilization of the latter, by self-moving spermatoid filaments set free from the former, takes place; and from the embryo-cell, which is the product of this operation, there arises—not, as in the Mosses and Liverworts, a conceptacle filled with spores, each of which may give origin to a separate plant,—but a single young Fern, which, having attained its full development by duplicative subdivision, detaches certain of its cells, as 'spores,' to continue the race by the same process. In this departure from the plan which prevails among the inferior Cryptogamia, we have an obvious *tendency* towards that of the Flowering-Plants: the entire product of each generative act being worked-up (so to speak) in the Fern, as in the Flowering Plant, into the diversified parts of a single organism; instead of being subdivided, as in the inferior Cryptogamia, amongst an indefinite number of independent fabrics, which are mere repetitions one of another. Still the *type* of the generative apparatus in the Ferns is essentially Cryptogamic.—That of the *Equisetaceæ* (Fig. 29) appears to be essentially the same; but in *Lycopodiaceæ* (Fig. 30), *Isoëtaceæ*, and *Rhizocarpeæ* (Fig. 31), there is a still closer approximation to the Phanerogamic type, the 'sperm-cells' ('small spores') being directly produced by the parent-structure, and the 'germ-cells' alone being evolved, after the detachment of the 'large spores,' upon the 'prothallium' into which each of these developes itself.

Fig. 31.

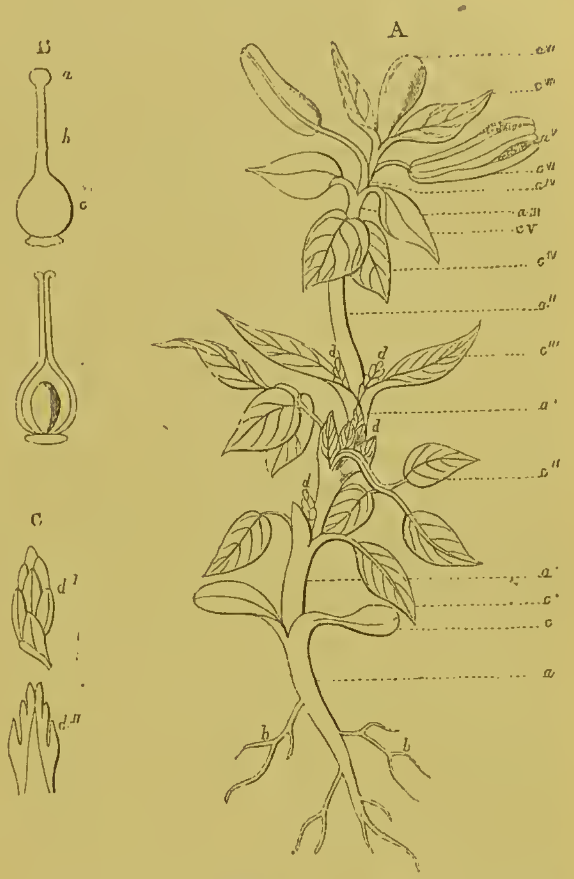


Marsilea quadrifolia.

29. The distinctive character of the PHANEROGAMIA or 'Flowering-Plants' is *not* the possession of what are commonly designated as 'flowers,' since these may be reduced to a condition in which they are scarcely distinguishable from the fructification of the Cryptogamia. In fact, the group of Rhizocarpeæ, in which the concurrent action of the small and large spores had been ascertained to be necessary for the production of an embryo, was referred by many Botanists to this division, at a period when the existence of distinct sexes had not been recognized among the Cryptogamia generally, and when it was, in fact, not merely doubted, but usually denied. Still, it is in the peculiar type of their Generative apparatus, that the essential distinction lies; for the fertilizing process is performed among them in a manner not elsewhere seen, namely, by the emission of a long tube from the 'germ-cell' (pollen-grain), which finds its way (often through a distance of some inches) to the 'sperm-cell' buried in the ovule; and it is among them alone that a true *seed* is produced, in which, with the embryo, a store of ready-prepared nutriment is laid-up for its early development. This sub-division of the Vegetable kingdom includes a vast range of species that differ very greatly in the degree of development, both of their nutritive and their generative apparatus; but for our present purpose, it will be sufficient to sketch the *typical* plan, which is more or less obviously manifested in the conformation of the entire group.—If we analyse the fabric of any common Phanerogamous Plant, we find that it consists essentially of an *axis* and *appendages;*

the former being made up of an ascending portion or *stem*, and of a descending portion or *root*, with their respective ramifications; and the latter being distinguishable into *foliaceous* and *floral* organs, which will be presently shown to be modifications of the same fundamental parts. The axis (Fig. 32, A, *a a*) is composed of cellular parenchyma, with a larger or smaller proportion of fibro-vascular tissue; and it is upon the mode in which these components are arranged relatively to each other, and in which progressive additions are made to the diameter of the axis, that the distinction is founded between the *Endogenous* and *Exogenous* types, which, together with corresponding distinctions in the structure of the leaves, flowers, and seeds, affords a basis for the sub-division of the Phanerogamia into two primary classes. From the central axis, bundles of fibro-vascular tissue pass down into the *root-fibres* which form the ultimate ramifications of its descending portion; these are enveloped in firm tissue, that limits their absorbent power to their extremities, which, being still soft and succulent, are known as 'spongioles.' On the other hand, the fibro-vascular bundles of the ascending portion of the axis pass into the footstalks of the *leaves*; and their ultimate ramifications form the skeletons of these organs, the interstices being filled up with cellular parenchyma, and the whole being clothed with an epidermis, quite distinct in texture from the parenchyma it covers, and perforated by the peculiar apertures termed 'stomata' (Fig. 155). Various modifications present themselves in the form of the leaves, and in the arrangement of their component parts; but none of these affect the essential character of the organs. The modes, too, in which they are arranged on the stem, present a great apparent variety; but they seem all reducible to one fundamental type, namely, a *spiral*, which is the result of the *radiation* of the appendages, not from a single

FIG. 32.



A, *Ideal Plant*, after Schleiden; a to a^{vi}, the axis, a being the root, a^{i}, a^{ii}, a^{iii}, a^{iv}, and a^{v} the successive internodes of the stem, and a^{vi} the terminal development of the axis into an ovule; b, rootlets; c to c^{vii} the successive foliaceous appendages to the axis, c being the cotyledons, c^{i}, c^{ii}, and c^{iii} the ordinary leaves, c^{iv} the outer floral leaves or sepals, c^{v} the inner floral leaves or petals, c^{vi} the stamens, and c^{vii} the carpellary leaves; d, leaf-buds:—B, carpel enclosing an ovule, seen externally and in section, showing a the stigma, b the style, c the ovary:—C, leaf-buds, as seen externally at d', and in section at d''.

point, but from a *longitudinal axis.* When this plan is characteristically exhibited, the leaves come off at regular intervals along the axis, but not in a vertical line one with another,—the second not being above the first, but a little to one side of it,—the third holding the same relation to the second,—and so on; in such a manner that a line carried through the points of origin of the successive leaves, which are termed 'nodes,' will not only ascend the stem, but will gradually turn round it, and will at last pass through a point directly above the origin of the first leaf. The leaves whose origin has been intersected by this line, whilst it makes one turn round the stem, are said to form a *cycle;* and the number of leaves which this cycle contains, is subject to great variations. Thus in *Dicotyledonous* plants generally it may be said to be *five;* that is, the sixth leaf will be directly above the first, the eleventh directly above the sixth, and so on. In *Monocotyledons,* however, the typical number is *three;* the fourth leaf being above the first, the seventh above the fourth, and so on. There are cases in which the cycle seems to consist of only *two* leaves; each leaf springing from the side of the stem precisely opposite to that from which the leaf below it, as well as the one above it, arises. The most common departures from the spiral type, shown in the disposition of the leaves, are those which are known as the *opposite* and the *verticillate* (or radiate) arrangements. These may be reconciled with it in three modes, each of which has some evidence to recommend it; and perhaps the deviation does not always take place in the same way.*

30. The complete *floral* apparatus of Phanerogamia consists externally of a 'perianth,' composed of a series of verticils of foliaceous organs, which do not depart widely, except in colour, from the ordinary type of the leaf, and are arranged according to the law of spiral development round the axis. For the first or outermost layer of the 'perianth,' in a perfectly regular flower, is formed of a whorl of bracts; the calyx is composed of a whorl of sepals (Fig. 32, c^{iv}) alternating with the preceding; and the corolla, in like manner, consists of a whorl of petals (c^{v}), which alternates with that of the sepals, but corresponds with that of the bracts. These whorls, in many flowers, are considerably multiplied, and the spiral arrangement of their component parts is often very obvious; and, when

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* Thus, 'opposite' leaves would be produced in a plant whose 'cycle' consisted only of two, by the non-development of every alternate segment, or 'internode' of the stem, so that each leaf and its successor on the opposite side come to be developed from the same part of the stem, whilst separated by an interval from the next pair. But this explanation does not suit those cases, in which the successive pairs of leaves are arranged on the stem at right angles to each other; and this arrangement may either be attributed to the development of two opposite leaves from each node, the successive pairs being then arranged in a cycle of four; or to the existence of two spirals proceeding up the stem simultaneously.—In like manner, a 'verticil' of five leaves originating from the same point of the stem, may be conceived to result from the non-development of the internodes between five successive nodes; and it sometimes happens that leaves which have a verticillate arrangement at one part of the stem, are spiral at another, being separated by the development of the intermediate internodes. But this does not account for the fact, that the successive whorls themselves usually alternate with each other; each leaf of the verticil being over the spaces between the leaves of the verticil beneath it.—And here again it would seem necessary, either to imagine that all the leaves of one verticil may originate from a single internode, or to suppose several spirals to be passing round the stem. In either way, however, this very common arrangement is reconcilable with the general theory of spiral development, which is thus readily carried into application as regards the disposition of the parts of the Flower.

such is the case (as in the Garden Pæony), we may observe such a gradual passage from the type of the ordinary leaf, through the succession of bracts and sepals, to the most characteristic petal, that the essential conformity of this last to the same general type with the preceding cannot be for a moment doubted. In the flowers of Dicotyledons, the typical number of components of each whorl, as of that of the cycle of ordinary leaves, is *five*, whilst in the Monocotyledons it is *three*. The regularity of a flower may be interfered-with by the suppression or by the multiplication of whorls; but the greatest departures from archetypal simplicity are those which result from the unequal development of different parts of the same whorl, some being very imperfectly evolved or even entirely suppressed, whilst others are extraordinarily augmented in size, and strangely altered in figure and character. The scientific Botanist, however, can seldom be at a loss in the investigation of their real nature, if he proceed on the morphological principles already explained; and he continually finds his determinations justified by the occurrence of 'monstrosities,' which exhibit a more or less complete reversion to the archetypal form (§ 82). The non-essential character of the perianth is indicated by the deficiency of one or more of its whorls in many tribes of Plants, which are nevertheless truly Phanerogamic. It is interesting to remark, however, that the group of *Gymnospermæ*, in which the deficiency is most complete, really form a transition-step to the higher Cryptogamia, in virtue of certain peculiarities in their proper generative apparatus, which will be explained hereafter (CHAP. XI).—It is within the protection of the perianth, that the true generative organs are developed; and these consist of the *anthers*, (Fig. 32, c^{vi}) from which the 'sperm-cells' (here termed pollen-grains) are evolved, and the *carpels* (c^{vii}), whose aggregation forms the *pistil*, containing the *ovules* (a^{vi}), each of which includes a 'germ-cell' imbedded in a mass of nutritious matter, the whole invested by two or more seed-coats. Now the anthers, which with their supporting 'filaments' constitute the *stamens*, depart more widely than do the sepals and petals from the ordinary condition of the leaf; but it is quite certain, alike from the history of their development, from the series of intermediate forms which some flowers (as the *Nymphœa alba*, or white water-lily) present, and from their occasional reversion in monstrous flowers to the form of petal or sepal, or even to that of the ordinary leaf, that they too belong to the same type of structure. The carpels (B), again, may be regarded as leaves folded together at the edges; as is indicated by their frequent retention of much of the leafy character, even in the normally-developed flower, and by their occasional more or less complete reversion to the type of the leaf in monstrous blossoms, sometimes when (as in the common 'double cherry') the stamens have undergone a less complete transformation. In the *Gymnosperms*, indeed, the carpellary leaves are not folded together so as to enclose the ovules, which are developed upon their internal surfaces; and merely protect them during their immaturity, by their own mutual adhesion.—It is the general rule for the two kinds of sexual organs to be developed in the same organism; and where, as is most commonly the case, every flower contains both stamens and carpels, it is said to be *hermaphrodite*. There are certain cases, however, in which, by the suppression of one or other of these whorls, the flowers become *unisexual;* when the staminiferous or male flowers are borne on the same plant or tree with the pistilline, it is said to be *monœcious;* whilst if the two sets of flowers are developed by different individuals, the species is said to be *diœcious.* This last arrangement, in which the generative apparatus attains its highest degree of differentiation, is comparatively infrequent; but we find examples of it in several groups of Cryptogamia, as well as among Phanerogamia.

31. The 'embryo-cell,' which is formed within the germ-cell, after the admixture of the contents of the sperm-cell with its own by the means already adverted-to, developes itself by duplicative subdivision, just as among the lowest Cryptogamia; but the nourishment which it requires for the continuance of this operation is furnished by the store previously laid-up in the ovule; and the entire mass of cells thus formed, instead of subdividing to constitute a multitude of independent organisms, remains connected so as to form but a single fabric; and this exhibits at a very early period a tendency to become heterogeneous, by the development of distinct organs, every kind of organ, however, being very numerously repeated. For, at the time that the seed is detached, as a self-sustaining structure, from the parent, the embryonic rudiments of the stem and root are already formed, and a temporary leaf-like expansion, the single or double cotyledon (Fig. 32, A, *c*), is prepared to evolve itself; whilst a supply of nutriment for its further development is stored-up within it, either forming a separate albumen external to the embryo, or being contained within its cotyledons, which are in that case thick and fleshy. The subsequent evolution of the plant, of which 'germination' is the first stage, consists in the progressive development of the ascending and descending axes and of their respective ramifications, these remaining permanent; and in the evolution, from the ascending axis, of a succession of mutually-similar appendages, foliaceous and floral, which have only a temporary existence, each set being in its turn replaced by another. Thus the individuality of the whole fabric is maintained, whilst a continual change is taking place in certain of its component parts.

32. It is with the performance of the true generative act, and the consequent production of a new embryo-cell, that each "new generation" originates. But it is not in this mode alone, that Phanerogamic Plants (for the most part at least) are multiplied. For each leaf-bud usually possesses within itself the capacity of putting forth roots, when separated from the parent-stock and placed in circumstances favourable to its growth, so that it thus becomes capable of maintaining an independent existence, and of developing itself into a perfect Plant; and there are some Phanerogamia which spontaneously detach leaf-buds or 'bulbels,' and which thus multiply themselves after a manner analogous to that which prevails so remarkably among the lower Cryptogamia. This is pre-eminently the case, for example, with the common *Lemna* (duck-weed), each plant of which consists of but a single foliaceous body, with a root-fibre hanging from its under surface; this puts forth buds from its margin; and these buds, early detaching themselves from their stocks, henceforth maintain an independent existence, so that the plant thus becomes rapidly multiplied by gemmation, large surfaces of water being covered by the growth proceeding from a single individual, without the intervention of any process of generation.—It is interesting to remark that this little plant seems to hold almost the same relation to

Phanerogamia, that the lowest Protophyta do to Cryptogamia. For it scarcely presents any distinction of parts, the leaf and stem being fused together into a single flattened lobe, whilst the organs of reproduction are reduced to their very simplest form, being developed in a slit in its edge. Its texture, too, is of the simplest kind, being composed of scarcely anything but ordinary cellular tissue. And the developmental process here, as in the Protococci, consists in the multiplication of organs which repeat each other in every particular, and which, having no relation of mutual dependence, can exist as well detached as coherent; instead of tending, as in the higher forms of Vegetable life, to the evolution of a single fabric, whose several parts present a marked differentiation of external form and of internal structure, and have such a functional dependence on one another, that they can only exist as living bodies so long as they remain mutually connected.

33. *Animal Kingdom.*—Turning, now, to the other great division of the Organised Creation, we shall in the first place examine, as in the previous case, what is the highest form under which its life expresses itself. The whole *nisus* of Vegetative existence consists in the activity of the organs of Nutrition and Reproduction; but, on the other hand, the *nisus* of Animal life tends towards the evolution of the faculties of Sensation and of Self-determined motion, and, in its highest manifestation, to that of the Intelligence and Will. The instruments of these faculties, however, are in the first place developed, and are afterwards sustained, by the Organic apparatus with which they are connected; whilst, in their turn, they become subservient to *its* operations: so that, in those forms of Animal existence, in which there is the greatest differentiation of organs, there is at the same time the closest relation of mutual dependence in their actions; and every thing tends to render the entire product of each generative act *a single individual*, in the most restricted sense of that term, no multiplication by the subdivision of that product ever taking place (save as a monstrosity), but the whole of it evolving itself into a congeries of different but mutually-related organs. It is only in the higher forms of Animal existence, however, that we meet with this complete individualisation, and this marked predominance of the *animal* over the *vegetative*. In a large proportion of the beings composing this kingdom, the apparatus which is subservient to the strictly animal functions is scarcely differentiated from that which ministers to organic life; in many of the cases in which the former is separately distinguished, it seems but a mere appendage to the latter; and it is only in the highest or Vertebrate type, that we find the general plan of the fabric distinctly arranged with special reference to the manifestations of Animal power, which involve the exercise of its highest attribute,—Intelligence. The nearest approach to this is made in the higher forms of the Articulated series; in which a very remarkable degree of development is given to the instruments of the lower animal powers, especially the locomotive apparatus; and in which the general plan of structure, and the arrangement of the nutritive apparatus, have evident reference to this. But in the Mollusca, we find a marked predominance of the Vegetative apparatus; it being in only a small proportion of the group, that there is any considerable power of movement. And in the Radiata, it becomes obvious that the general plan has reference rather

to the 'vegetative repetition' of the organs of Nutrition and Reproduction, than to any manifestation of the higher Animal powers; the apparatus for which, in so far as it is developed, exhibits a like repetition of similar parts.—Notwithstanding the diversity of these types of structure, however, and the marked differences which they present in regard to the relative development of their several organs, we observe in the higher forms (at least) of each of them, a differentiation of all the most important parts by which the Animal is especially characterised. For we find in each type a *digestive cavity* for the reception and preparation of aliment; *chyliferous channels* or *vessels*, into which the liquid prepared by the digestive process transudes from this cavity, to be conveyed to the remoter parts of the organism; a *circulating system*, by which the distribution of the nutritive fluid is effected, the surplus materials brought back, and the waste or refuse matter removed from the tissues and conveyed for elimination to appropriate organs; a *respiratory surface*, through which the circulating fluid is exposed to the influence of atmospheric air; *secreting glands* for the separation of certain products from the blood, either for *its* purification, or for special uses in the economy, or for both purposes combined; *generative organs*, in which 'sperm-cells,' or 'germ-cells,' or both, are developed, the latter being enclosed (as in Phanerogamous Plants) in a store of nutriment prepared for the nutrition of the germ, so as to constitute an *ovum;* organs of *support* and *protection*, forming a 'skeleton' of some kind, either external or internal; organs of *sensation;* organs of *consciousness* and *self-direction;* and organs of *locomotion.*

34. It is true that in the least-developed forms of each type, we may find some or other of these organs but little distinguished from the general structure, or even entirely absent; but the proportion of such forms is smaller, the higher we ascend in the scale. Thus, in a large part of the *Radiated* series, there is but little differentiation of the several parts of the nutritive apparatus; and although the reproductive is nearly always very distinct from it, yet even this is scarcely segregated in the lowest examples of the type: whilst even the very slight development which the organs of animal life attain in the higher Radiata, is altogether wanting in the lower, among which they are not distinguishable by any structural mark.—But in the *Molluscous* series, it is only among the very lowest that we have a difficulty in distinguishing all the essential parts of the apparatus of nutrition and reproduction, the absorbent and circulating apparatus being usually that which is most imperfectly developed; and although the organs of sense and locomotion are not evolved in the same proportion, we never fail to find a nervous ganglion, which must be considered as marking the existence of some degree of consciousness.—On the other hand, in the lowest forms of the *Articulated* series, it is the imperfection of the nutritive apparatus which most strikes us; and although distinct sensori-motor organs are there also very deficient, yet they present themselves very prominently in higher parts of this series, in which the type of nutritive system is still comparatively low. In both these sub-kingdoms, however, it is only in a small proportion of each series respectively, that we fail to discern all the essential parts of the assemblage of organs just now enumerated; those higher forms of each, in which the differentiation is complete, constituting the great bulk of its entire series, instead of being, as among the

Radiata, exceptional as to number, and probably to be so considered in regard to type likewise.*—Now, in the *Vertebrated* series, the complete differentiation of all these structures is nearly the invariable rule; it being only in one of the very lowest Fishes (the *Amphioxus*), that we meet with such an imperfect development of any of the systems above enumerated, as reminds us of those simpler organisms in which they are absolutely deficient.—There is another point of interest nearly related to the preceding, in regard to which these primary types of Animal conformation present a marked contrast; and this is the degree in which they are severally capable of being multiplied by gemmation. This power exists among Zoophytes in exactly the same degree as among the higher Plants; for, whilst the gemmæ, in the former as in the latter, usually remain connected with the parent-stock, they are capable of maintaining their existence if detached, and are regularly thrown-off in some species, so as to become independent organisms, possessing all the capabilities of that from which they have separated themselves; and in the very simplest Zoophytes (as the Hydra), we even find a capacity for reproducing the entire fabric to lie in every fragment of the body, just as a fragment of the leaf of Bryophyllum will give origin to an entire plant (§ 21, note). A like capacity exists in the lowest group of the Mollusca, which, in this and in many other particulars, closely borders upon Zoophytes. It is only among a very small number of the lowest Articulated animals, however, that this method of multiplication presents itself. And among Vertebrata it seems entirely wanting as a regular habit, although there is reason to think that it may occasionally occur as an abnormality, at that early period of the evolution of the germ when its grade of development has not advanced beyond the Zoophytic stage (CHAP. XI.)

35. Underlying these well-marked types of Animal organisation, however, there is a group of beings which cannot be regarded as presenting even a rudiment of the plan of conformation that is characteristic of any one of them, and in which scarcely any differentiation of organs is to be discerned,—a group, in fact, which holds a rank in the Animal kingdom, that is precisely parallel to that of the *Protophyta* in the Vegetable (§ 22), and which may therefore be appropriately designated PROTOZOA. Between these two groups, indeed, no definite line of demarcation can be drawn; and the same beings have been reckoned as Plants or as Animals, according to the particular views of the classifier in regard to the mode in which they should be distinguished. A large proportion of the Protozoa consist of single cells, or of aggregations of cells in which there is no differentiation of character; and in the lowest forms of them, there is not even that distinctness of the cell-wall from the cell-contents which exists in every completely-developed cell, but the whole forms one mass of living jelly (Fig. 33). The animal character of this, however, is marked in its mode of nutrition; for it does not draw its aliment, like the Protophytes, from the surrounding air and moisture, but is dependent for its support upon organic substances previously elaborated by other beings, which it envelopes with its own jelly-like substance, and of which it gradually dissolves and appropriates that which is fitted for its own

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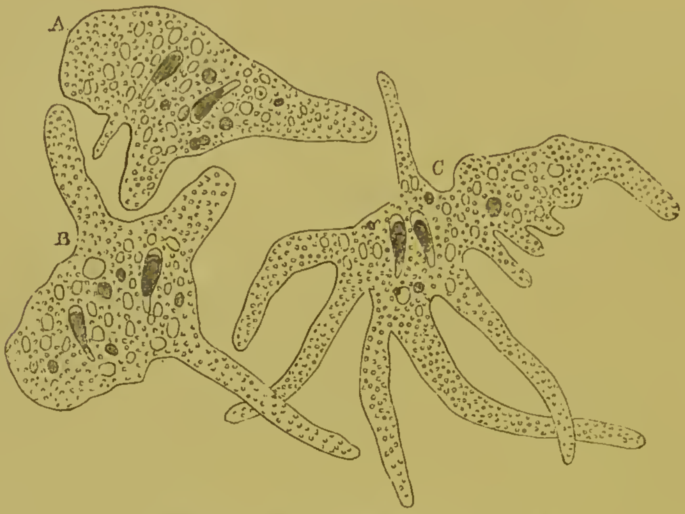
* In the Author's opinion, the *Zoophytes*, not the Echinodermata, are the types of the *Radiated* series;—*Gasteropods* of the *Molluscous;*—*Insects* of the *Articulated;*—and *Mammals* of the *Vertebrated.*

increase. The animal character of this body is also indicated by its movements; for although the 'zoospores' of the Protophyta and lower

FIG. 33.



Amœba princeps, in different forms, A, B, C.

Algæ are rapidly propelled through the water by ciliary action, yet they do not exhibit that motion of one part upon another, which is often seen in the simplest Protozoa. But there are as yet no *special* instruments either for sensation or for motion. As every part of the body is equally adapted for digestion, for absorption, for circulation, for respiration, and for secretion, so does every part appear equally capable of receiving impressions made upon it, and of responding to them by a contractile movement. From this starting-point we may proceed in either of two directions; for we find in the *Infusory Animalcules* a tendency to the individualisation of the single cell, which seems to attain in them its highest development as a separate entity; whilst in the *Rhizopoda* (Foraminifera) and *Porifera* (Sponges) we find aggregations of gelatinous bodies (which present more or less distinctly the characters of true cells) assuming certain definite types of form, and approaching the individuality of higher organisms.—In the true *Animalcules* (excluding the Rhizopods and the Protophyta which have been confounded with them) we find an obvious distinction between cell-wall and cell-cavity; there is a definite opening into the latter, through which food is introduced, instead of its being received into any part of the mass; and there is frequently, also, a second orifice, through which indigestible particles are expelled. Moreover, the locomotion of these beings is performed, as in the Protophyta, by the agency of *cilia;* these being prolongations of the cell itself, to which the contractile power is especially delegated. Their multiplication is ordinarily accomplished, like that of the Protophyta, by duplicative subdivision; and in this way a vast number of similar beings may be produced, each of which is a repetition of the rest, and lives altogether independently of them. But it seems probable that, like the Protophyta, they have a proper generative process, consisting in the 'conjugation' of two similar cells; no sexual distinction as yet manifesting itself between these, and both of them apparently contributing in the same manner and degree to the production of the germ.—In the *Rhizopoda*, we find the simple jelly-like mass extending itself by gemmation, and at the same time very commonly forming a calcareous envelope upon its exterior; whilst through apertures in this are put forth extensions (*pseudopodia*) of the soft substance in its interior, through which the introduction of nutriment into the body seems to be chiefly effected. Notwithstanding the small amount of differentiation which appears to exist among the several products of gemmation, yet a strong tendency to individualisation in the entire aggregate is shown in the very definite plan of growth which each species exhibits, as is most obviously seen in *Nummulites* and other higher forms of Foraminifera. Of the mode of multiplication of these animals, nothing is yet known.—In the *Porifera*, or Sponges, there is, with less definiteness of configuration in the aggregate mass produced by gemmation from the single primordial cell, a much higher degree of mutual interdependence; for we now find the component particles so arranged as to form the rudiments of differentiated organs, whilst the general plan of structure approaches that which we meet-with among the lower Zoophytes, in whose fabrics the individuality of the components is still more completely merged in that of the organism as a whole. For, in the first place, we have a marked distinction between the internal fibrous skeleton and the soft flesh which clothes it; and these components have a very definite and characteristic arrangement, which varies in different parts of the mass; being dissimilar, near the external surface, and around the internal canals, to that which prevails in the intervening substance. Again, in the system of absorbent pores for the entrance of liquid, and of ramifying canals for its discharge, we have the first rudiment of a digestive and circulatory apparatus, not yet marked-off, however, from the general cavity of the body. And although the organs of nutrition do not present any further specialisation, yet those of reproduction are differentiated from them, and are limited to particular parts of the mass. Even in this lowest form of an aggregate Animal, there is reason to believe that a true *ovum* is produced; so that we here already advance to the same essential type of generation, as that which prevails in the highest plants.

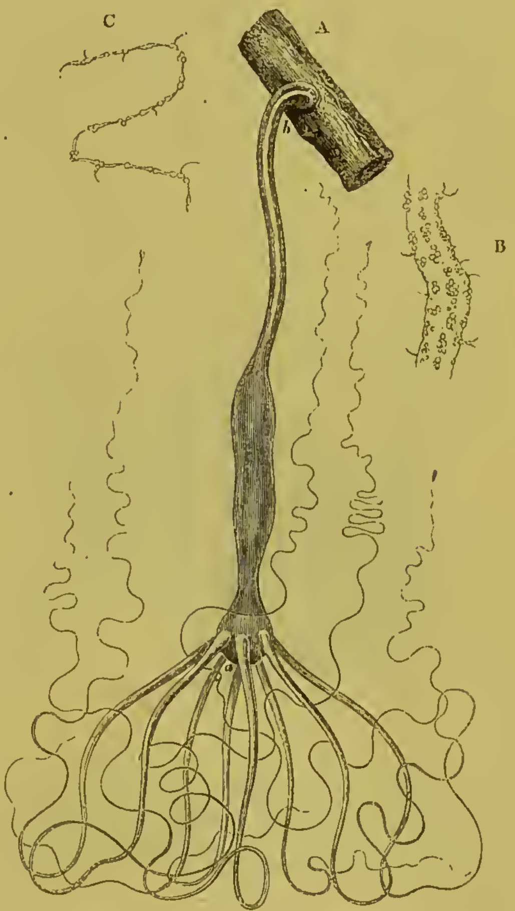
36. Among the four definite types of structure under which all the higher forms of Animal organization may be ranked, the **Radiated**, as already remarked, unquestionably holds the lowest rank: in virtue alike of the close conformity of its general plan to that which prevails in the higher Plants; of that predominance of its Vegetative or Nutritive apparatus over that of Animal life, which is conspicuous even in its higher types; and of that very imperfect differentiation of the organs of the former, which prevails through the larger part of the group. Each of these points will now be noticed in some detail.—The *radial symmetry* must be regarded as in itself a vegetative character, for it corresponds with that which is seen in the disposition of the appendages around the axis in the leaf-buds and flower-buds of plants; and it is intimately connected with another vegetative character, the *repetition of similar parts*. Thus, in the animals in which it prevails, we find the central mouth to be surrounded externally by a circular series of prehensile appendages; which may be mere oral tentacles, as in the *Polypes* (Figs. 34, 35), the *Medusæ* (Fig. 93), and the *Holothuria* (Fig. 40), true

arms, as in the *Ophiura* and *Comatula* (Figs. 8, 38), or divisions of the body itself, as in the *Star-fish* (Fig. 37). In the arrangement of the internal organs, a similar character is exhibited; that is, a circular disposition of parts which precisely repeat each other. There are, it is true, modifications of the radial type in certain aberrant forms of the group, which tend towards a bi-lateral symmetry; but these are comparatively rare exceptions, which it is only necessary here to mention. It is not only in their radial symmetry, however, that the animals of this division are conformable to the type of the higher portion of the Vegetable kingdom; for this conformity is equally shown by a large proportion of the group, in the development of composite structures by gemmation. From a single polype, as from a single leaf-bud, an arborescent structure may be evolved, bearing hundreds or even thousands of polype-bodies, all originating from the first, and maintaining an intimate organic connection with each other; thus bearing a close physiological resemblance to a tree, and requiring to be considered (like it) as a single individual, although its several members have no relation of mutual interdependence, and can maintain a separate existence if detached. It is not to be wondered at, then, that the older Naturalists, who were only acquainted with the skeletons of Zoophytes, should have considered them as vegetable structures, and that many of them should even now be popularly regarded in that light; whilst even the movements exhibited by the living polypes, not being apparently very different in nature from those performed by the Sensitive-Plant, or the Venus's Fly-trap, did not seem sufficient to establish their animal nature. This extension of the original fabric by gemmation may take place among Zoophytes to an indefinite extent; and the mode in which it occurs is the chief determining cause of the particular type or plan of growth which is traceable in each species, but which is liable to great variation from the influence of external conditions. In nearly all the members of the class of *Acelephæ*, it seems to take place at some period of life or other; for although we find few traces of it in the fully developed *Medusæ*, yet (as will be shown hereafter, CHAP. XI.) multiplication by gemmation takes place to an extraordinary extent during the early stages of their existence; and in some of the lower forms of the group, especially those which closely approximate to the Zoophytic type, it continues during the whole of life, and gives rise to those composite fabrics of the *Cirrhigrade* and *Physograde* orders, which, until the recent discovery of their true character, have been a source of so much perplexity to Naturalists. In the class *Echinodermata*, multiplication by gemmation very seldom takes place; but its members retain throughout their lives an extraordinary measure of that power of reproducing lost parts, of which the production of an entire organism by gemmation is only a higher manifestation.

37. The low development of the proper Animal powers in Radiated animals, as compared with their Vegetative activity, is one of the most remarkable features of the group taken as a whole; nor are there are any exceptions to this general character. In none of the true *Zoophytes* is the nervous system differentiated from that general fibro-gelatinous tissue of which the entire bodies are composed; every part seems more or less impressionable and contractile, although these attributes are most strongly displayed in the oral tentacula; and there is no evidence that

the respondence to external impressions which is probably the source of all their movements, proceeds from any distinct consciousness of these impressions. It is in the *Acalephæ*, that the first traces present themselves of a nervous system, and of organs peculiarly fitted to receive sensory impressions; but it is probable that a large part of the movements executed by even these animals, are not dependent upon any influence transmitted through this apparatus. In the *Echinodermata*, whose organs and tissues attain a far higher grade of development, the nervous system is more clearly marked out; and the distinction between nerve-cords and ganglionic centres, which has not yet been clearly established in the Acalephæ, may be unmistakeably affirmed to exist. There are also rudiments of eyes in certain members of this class; and there is some evidence that their movements are directed by visual impressions received through these organs.

FIG. 34.

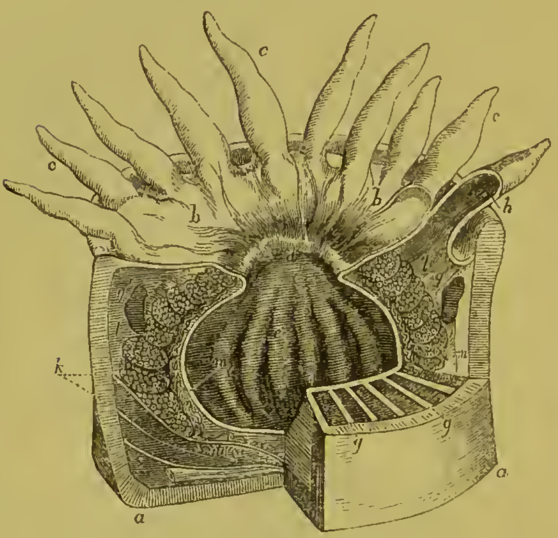


A, *Hydra fusca*, or Brown Fresh-water Polype, attached to a piece of stick, with its arms extended, as in search of prey; *a*, the mouth surrounded by tentacula; *b*, foot or base, with its suctorial disk: at B is seen a portion of one of the arms near its origin, and at C another portion near its termination, more highly magnified.

38. Between the lowest and the highest members of the Radiated series, there is a very marked contrast in regard to the differentiation of the principal organs of Vegetative life; but a number of intermediate gradations present themselves, which establish a tolerably complete transition from the one condition to the other.—Commencing with the *Hydra* (Fig. 34), we find the digestive apparatus reduced to a state of the greatest simplicity, the whole body seeming to be nothing else than a stomach, with a circle of prehensile tentacula around its orifice, which, being single, and serving alike for the reception of food and for the ejection of its indigestible portions, must be considered as representing in itself the cardiac and pyloric orifices of the stomachs of higher animals. The wall of this cavity and the general integument of the body are so closely connected together, as to seem like two layers of one and the same membrane; there are, however, some lacunar spaces between them, constituting the first indication of that 'general cavity of the body' which exists in almost every other animal, and which performs, as we shall see, very important functions; and these lacunar spaces communicate

with similar cavities in the interior of the tentacula. There does not yet appear to be any decided structural or functional differentiation between the layer which lines the stomach and that which clothes the body; since each can perform all the offices of the other, as is shown by the result of Trembley's well-known experiment. No circulating apparatus is yet distinguishable, the nutritive liquid, which is the product of the digestive operation, being at once absorbed from the parietes of the stomach into the general substance of the body and arms; nor is there any special respiratory or secretory apparatus. Even the generative organs, which are usually the first to be differentiated from the rest of the fabric, cannot here be distinguished; for ovules and sperm-cells are evolved in the substance of the ordinary tissue; and the only indication of their specialization is afforded by the restriction of their production to particular situations, the sperm-cells usually making their appearance just beneath the arms, whilst the ovules protrude nearer the foot. The homogeneousness of the entire body, however, is most remarkably evinced in the facts, that *gemmæ* which develope themselves into new Hydræ sprout almost indifferently from any part of it, and that a minute fragment from any region will (under favourable circumstances) regenerate the whole. In the composite fabrics which are formed after the Hydraform type (Fig. 99), the consolidation of the external integument necessitates several other changes; amongst the rest, the evolution of a special reproductive apparatus, and the separation (within the polype-cells) of the wall of the stomach from the external integument, so as to commence the formation of the 'general cavity of the body.' This, however, is carried much further in the *Actinia* (Fig. 35), and in all the Polypes formed upon its type; for in these we find the stomach suspended (as it were) in a large space, which is subdivided by radiating partitions; and it is in the chambers thus formed (which are prolonged into the interior of the tentacula) that the generative apparatus is situated. Very distinct organs for the production of sperm-cells *or* of ova are here evolved; these organs (according to late researches, CHAP. XI.,) not being combined in the same individuals. There is still a direct connection between the interior of the digestive sac and the general cavity of the body, by an aperture at the bottom of the former; and through this, the nutritive products of digestion find their way into the surrounding cavity, mingled with the

FIG. 35.



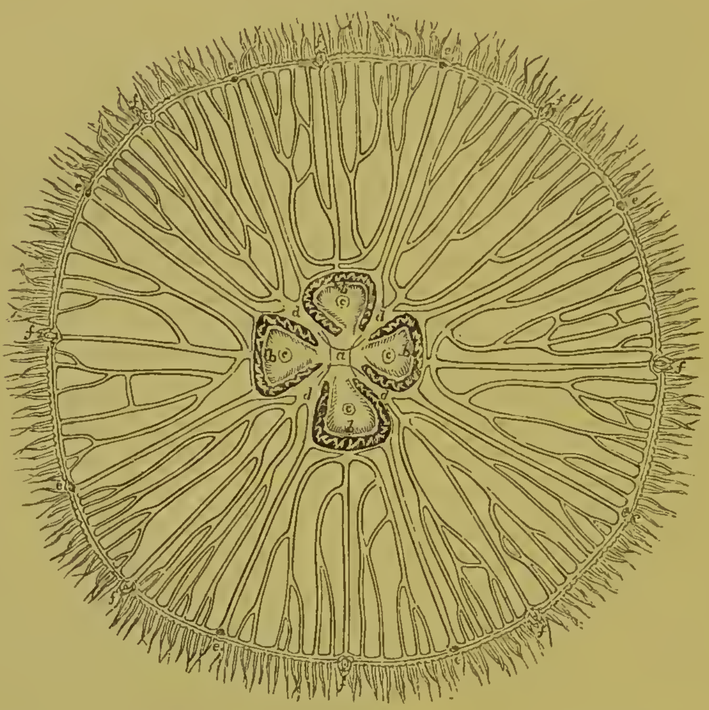
Diagrammatic section of *Actinia*, showing its interna structure;—*a*, *a*, base or foot; *b*, *b*, oral disk; *c*, *c*, tentacula; *d*, mouth; *e*, stomach; *g*, *g*, *k*, *k*, vertical partitions cut across in different directions; *g′*, *g′*, apertures in these; *h*, passages opening into the tentacula; *l*, *l*, testes or ovaria; *m*, *m*, filiferous filaments.

water which is introduced through the mouth. This is the only mode in which the tissues are nourished, as there is not yet any special circulating apparatus; and, in like manner, it is only by the expulsion of the fluid that has remained for some time in the general cavity, that the excretory products which have found their way into it from the tissues, can be carried out of the body, in those species which have no orifices at the extremities of the tentacula. Thus the very same liquid answers all the purposes, in these simply-formed animals, which are served in Vertebrata by chyme, chyle, arterial blood, and venous blood; and it also serves as a medium for respiration, the external integument being usually so thickened and hardened, that the amount of aëration of the interstitial fluids which takes place through it must be extremely limited, in comparison with that which will be carried on through the delicate membranes clothing the internal surfaces. Thus, with some very important points of differentiation, the general type of these animals remains extremely low; and their power of multiplying by gemmation, and of reproducing lost parts, in which they are only inferior to the Hydra, is what we might anticipate from their general homogeneousness. In the composite *Actiniform* Zoophytes, a certain degree of connection remains between the general cavities of the Polypes which have budded-off one from another; but this connection is more intimate in the *Alcyonian* Zoophytes (Fig. 100), among which the 'general cavity' extends throughout the polypidom, forming a branching system of canals which strongly resembles that of Sponges. In fact, when we compare the two organisms, we can scarcely fail to perceive that the Alcyonium is essentially a Sponge of which certain parts have been differentiated from the rest, and evolved into special organs. And this view is confirmed by the circumstance, that when a bud is put forth from one of those polypidoms, it has all the ordinary characters of a Sponge, except that its canals do not open upon the external surface (Fig. 91); the formation of a polype-mouth and stomach not taking place until a later period.

39. The lower forms of the class of *Acalephæ* carry us back to the grade of development proper to the composite Hydraform Zoophytes. But in the higher, such as the ordinary *Medusa* (Fig. 36), there is a far less amount of repetition of similar parts, the gemmæ detaching themselves from each other at an early stage of development, and subsequently maintaining an entirely independent existence. There cannot be here said, any more than in the Hydra, to be any 'general cavity;' for the space between the walls of the digestive sac and of the ovarial chambers which surround it, and the external integument, is occupied by homogeneous solid tissue. But a series of gastro-vascular canals, commencing from the stomach, radiates towards the margin of the disc; and these serve the double purpose of conveying the nutritive product of the digestive operation to the remoter parts of the body for the supply of their wants, and of subjecting it to the aerating influence of the surrounding medium. In its return to the centre, the fluid will of course carry back with it whatever excretory products it may have received from the tissues through which it has passed; and thus, like fluid of the stomach and general cavity of the Actinia, it answers to the chyme, chyle, arterial blood, and venous blood, of Vertebrated animals. In the *Beroe* (Fig. 102), and certain allied forms, the digestive cavity has an anal as well as an oral

orifice; and there also appears reason to think, that in its system of gastro-vascular canals a difference already exists between the afferent and efferent tubes, the fluid passing forth from the stomach by one set, and returning to it by the other. The generative apparatus in this class always exhibits a very well-marked differentiation; its type being in many respects higher than that of the true Zoophytes. For in the Medusa, the four ovaries or testes (*b*, *b*) are lodged in cavities round the mouth, each of which has its own proper outlet (*c*, *c*), so that the mouth is no longer (as it is in those species of Actinia the extremities of whose tentacula are closed) the only channel for the escape of the fertilized ova or of the rudimentary young. The sexes are here distinct, the ova and testes not being combined in the same bodies: and this is true also of many of the composite forms, which develope medusa-like buds containing sexual organs, each individual producing buds of only one sex, as in diœcious plants; in others, however, male and female medusa-buds are developed on the same stock, as in monœcious plants, although in no case are the two sets of generative organs combined in the same medusoid body.

FIG. 36.

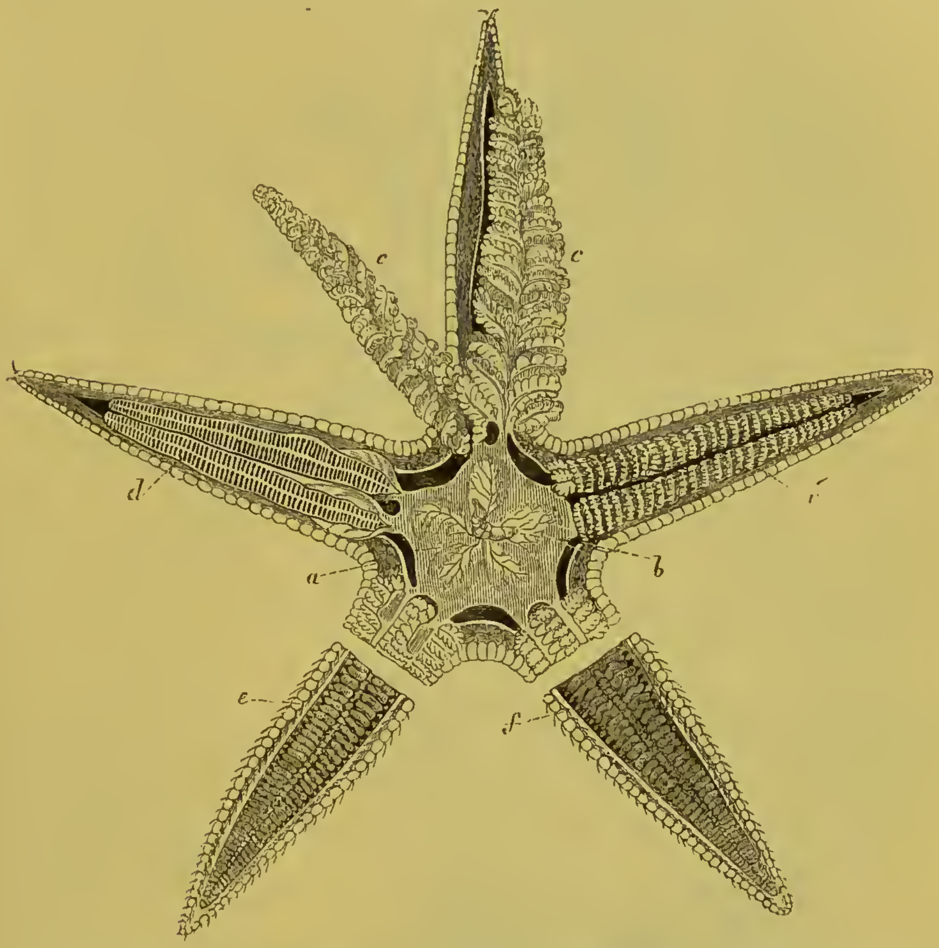


Structure of *Cyanæa aurita.*—Disk seen from above, showing the quadrilateral mouth *a*, the four ovaries *b b b b*, the four orifices of the ovarian chambers *c c c c*, the stomach *d d d d*, and its radiating prolongations, the eight anal [?] orifices *e e*, &c., and the eight ocelli [?] *f f*, &c.

40. In the class *Echinodermata*, the *Asterias* (Fig. 37) holds by no means an elevated rank; yet we find in it a very marked advance upon either of the types previously described. The stomach with its single orifice, suspended in the midst of the 'general cavity of the body,' reminds us of that of Actinia; but it is entirely cut off from that cavity, which consequently remains closed. The nutritive products of digestion probably find their way into it, however, by transudation through the

walls of the stomach; and it is thence taken up by a regular system of vessels, the distribution of which, however, is very limited, so that the fluid of the general cavity seems still to take the largest share in the nutritive operation. It is interesting to remark, that in this class we already meet with a differentiation, however imperfect, not only between the fluid of the gastric cavity, or *chyme*, and that of the surrounding visceral cavity, or *chylaqueous fluid*,* but also between the latter and the

FIG. 37.



Asterias aurantiaca, with the upper side of the hard envelope removed:—*a*, central stomach; *b*, cæca upon its upper surface (salivary glands ?); *c c*, cæcal prolongations of the stomach into rays ;*c′*, the same empty; *d*, the same laid open; *e*, the under surface, seen from within after the removal of the cæca, showing the vesicles of the tubular cirrhi; *f*, the same in a contracted state, showing the skeleton between them.

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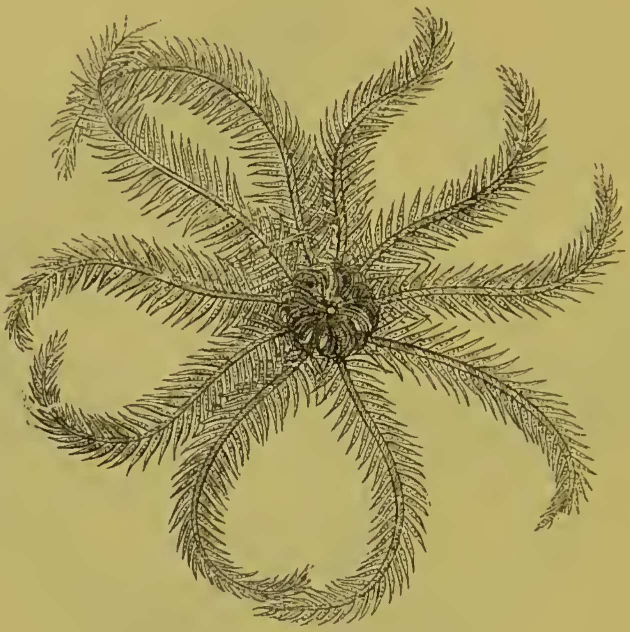
* The term *chylaqueous fluid*, introduced by Dr. T. Williams, appears to the Author to be well adapted to designate the fluid of the 'general cavity,' when (as in Echinodermata and Annelida) this is distinct alike from that of the digestive sac, and from that of the proper circulating system. It is far more extensively employed, however, by Dr. Williams in his ingenious Memoir 'On the Blood proper and Chylaqueous Fluid of Invertebrated Animals,' in the "Philos. Transactions," 1852; being there applied to the immediate product of gastric digestion which passes directly into the 'general cavity' of the Actiniform and Alcyonian Zoophytes, and even to that which is confined within the stomach and gastro-vascular canals of Medusæ.

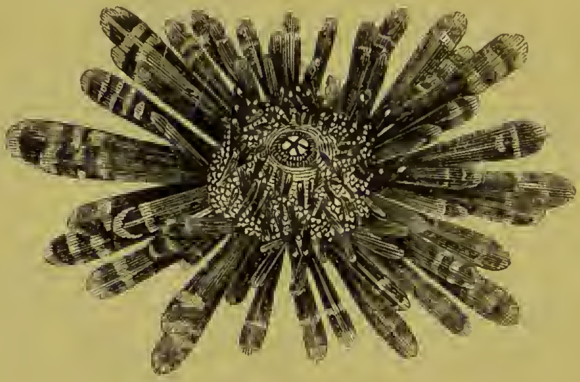
blood contained within the proper circulating system. A special provision appears to be made for respiration in these animals, by the transmission of the 'fluid of the general cavity' into a multitude of short delicate cæcal tubes, which pass between the pieces of the calcareous framework and project externally in little tufts, and which are lined with cilia that keep up a constant movement in their contents. And there are various secretory organs possessing a distinct glandular character, whose special uses are not yet certainly known. The generative apparatus here attains a high development, the ovaries and testes (as in the higher Acalephæ) being no longer combined in the same individuals, and having separate orifices for the discharge of their products; it is interesting to remark, however, that in *Comatula* (Fig. 38), whose digestive apparatus is framed upon a higher type than that of Asterias, the ovaries are dispersed in isolated spots through the integument of the arms. The Star-fish exhibits a series of elaborate provisions for locomotion, in the beautiful articulation of the plates of the calcareous skeleton, in the contractility of the general integument of the body, by which its lobes (misnamed 'arms') are moved in various directions, and in the multipli-

Fig. 38.



Comatula rosacea.

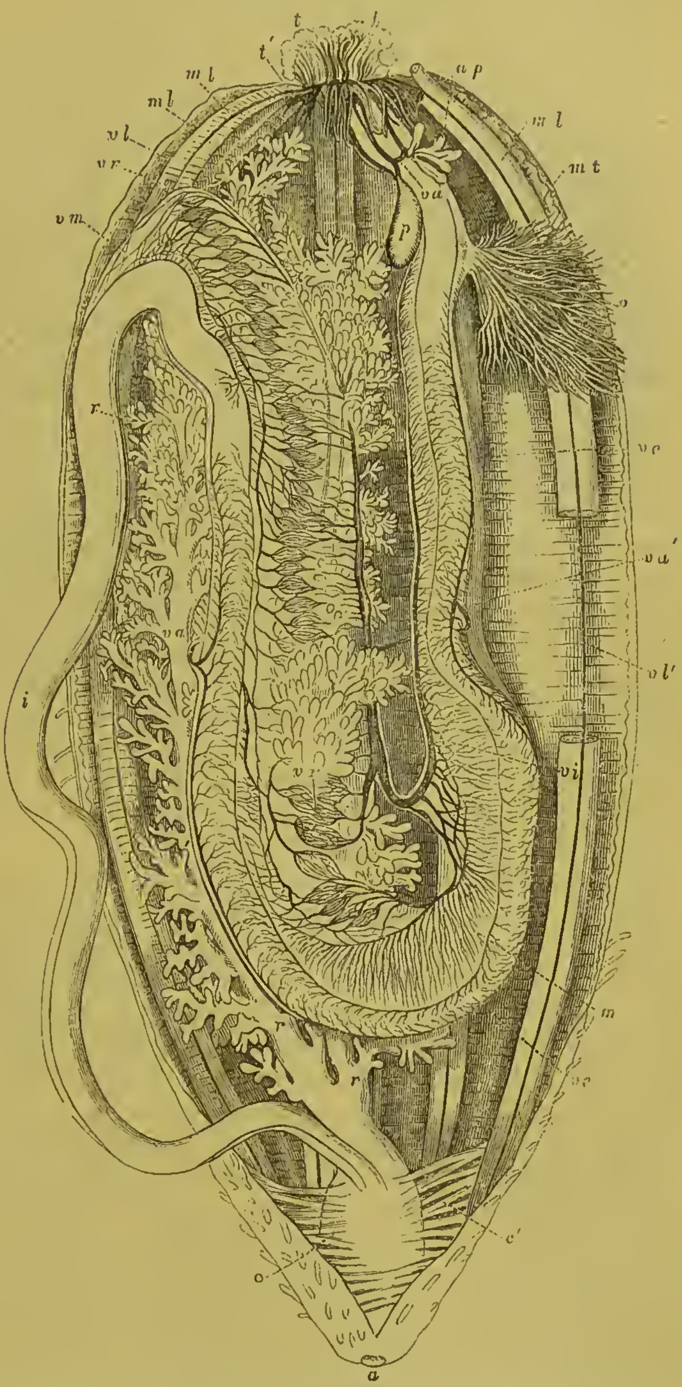
Fig. 39.



Echinus mammillatus.

cation of tubular *cirrhi* furnished with suckers, by the contraction of which, when the suckers (forced out by the injection of fluid into the cirrhi from the 'general cavity') have taken an attachment, the body is drawn towards the points to which they have adhered.—The chief feature of advance in the *Echinus* (Fig. 39) is the conversion of the digestive sac with a single orifice, into an alimentary canal with a separate mouth and anus; and around the mouth we find a very elaborate dental apparatus, furnished with distinct muscles, such as do not make their appearance in any lower forms of organisation. The locomotive apparatus, too, is still more highly developed; for the body being now enclosed in an immovable case, so that its parts are not themselves capable of flexure, a new set of instruments is evolved, namely,—the calcareous

FIG. 40.



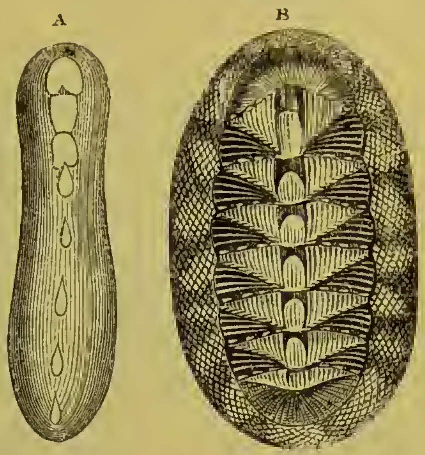
Anatomy of *Holothuria tubulosa*;—*a*, anus; *b*, mouth, surrounded by 20 tentacula; *c*, cloaca, surrounded by muscular dilators *c'*; *i*, intestinal tube; *m*, mesentery; *ml*, *ml*, longitudinal muscles; *mt*, transverse muscles lining the entire inner surface of the integument; *o*, ovary; *ap*, cæcal appendages, probably seminiferous; *p*, contractile vesicle, probably a heart; *r*, *r*, respiratory apparatus, originating in the cloaca; *t*, oral tentacula; *t'*, cæcal reservoirs; *va*, annular vessel surrounding the mouth and supplying the tentacula; *ve*, external intestinal vessel, giving off a large anastomotic branch *va'* which enters another part of the same trunk; *vi*, internal intestinal vessel, with contractile dilatations; *vl*, longitudinal tegumentary vessel, giving off transverse branches *vl'*, seen by removing the longitudinal muscles; *vm*, mesenteric vessels, connecting the branches of the external intestinal vessel with those of the respiratory system of vessels, *vr*.

spines, which project from the surface, and are put in motion by the contractile integument, upon the ball-and-socket joints at their base. —The *Holothuria* presents us with certain interesting features of more complete differentiation, without, however, any very decided advance upon the type of the Echinus. The absence of a solid 'test' enables its movements to be performed by the flexure of the body generally; and for this a regular series of longitudinal and transverse muscular bands (Fig. 40, *m l*, *m t*,) is provided, reminding us of those of the Worm-tribe. The alimentary canal (*i*) does not yet present any distinction of parts into œsophagus, stomach, or intestine, but remains of nearly the same diameter throughout its length; it is held in its place in the midst of the general cavity of the body, however, by a regular mesentery, upon which the blood-vessels are minutely distributed. The circulating system is more complete than among other members of this class, especially in its peripheral portion; and it is furnished with a pulsatile vesicle (*p*), whose contractions assist the onward movements of their fluid. For respiration there are two special provisions; the fluid of the circulatory vessels being aerated by transmission to the branching oral tentacula (*t*); whilst that of the 'general cavity' receives the same influence from the water introduced through the respiratory tree (*r*, *r*). The restriction of the outlet of the genital apparatus (*o*) to a single aperture (the five equal and separate portions of this apparatus in the Echinus and Asterias having each its own outlet) is a very decided character of elevation; which seems to have been presented also by the extinct group of *Cystidea* (Fig. 81), notwithstanding that in the attachment of these animals by a stalk to a fixed basis, they (in common with the Crinoidea) showed a decidedly zoophytic tendency.

41. The MOLLUSCOUS sub-kingdom, like the Radiated, is remarkable for the high development of its apparatus of *vegetative* life in comparison with that of *animal* life; but its type of conformation is altogether different. It is true that, in the lowest group of this series, there is such a close *apparent* conformity to the Zoophytic type, that the animals belonging to it were, until recently, unhesitatingly ranked under that designation. But it is now perceived that the resemblance is only superficial; being dependent, in part upon the mode in which these animals extend themselves by gemmation, so as to form arborescent structures very analogous to those of true Zoophytes; and being partly caused by the state of degradation to which various organs are reduced, whereby their true type is obscured.—Taking it as a whole, the Molluscous series is characterized rather by the absence, than by the presence, of any definite or symmetrical form. In the Zoophytoid Mollusks, it is true, we are reminded of the *radiated* type by the circular arrangement of organs around the mouth (Fig. 49, *a*); whilst in the family of *Chitonidæ*, we meet with a division of the external skeleton into segments (Fig. 41), which reminds us of the *articulated* type. But these are peculiar exceptions; and a Molluscous animal is essentially a bag of viscera, enveloped in a skin which is thickened in parts by muscular fibres that are not arranged after any constant plan. In the 'archetype' Mollusk, the mouth and anus are situated at the two extremities of the sac; and the various organs are disposed symmetrically on the two sides of a longitudinal

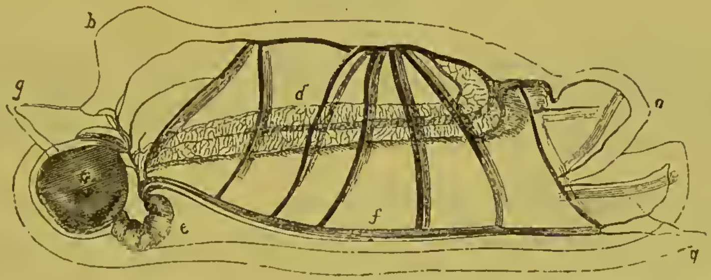
median plane, just as in a Vertebrate or Articulate embryo; the centres or principal trunks of the circulating apparatus being on the dorsal aspect (which may hence be termed the 'hæmal'), whilst the principal centres and trunks of the nervous system are on the ventral aspect (which may hence be termed 'neural'.) But this simple and symmetrical arrangement is very commonly obscured by subsequent inequalities in the development of particular regions, so that an entire change takes place in the relative position of the different organs, and the types of conformation thus evolved *seem* to have little or no affinity to one another.[*] — The nearest approach to the archetype is presented on the whole by those of the *Tunicata*, in which the two orifices retain their original positions at the poles of the body (Fig. 42); and their chief peculiarities consist, in the first place, in the enormous development of their pharynx to form the branchial sac, and secondly, in the inversion of their integument around the anal orifice, so as to form an immense cloacal cavity, the wall of which extends so far into the interior, and so completely envelopes the general mass of the body, as to constitute what is known as their 'inner tunic.'[†]—In the *Bivalve* Mollusks, on the other hand, the principal extension of the integument takes place externally; a duplicature of the thickened glandular skin of the 'dorsal' or 'hæmal' region

Fig. 41.



A, *Chitonellus*.—B, *Chiton*.

Fig. 42.



Salpa maxima; *a*, oral orifice; *b*, vent; *c*, nucleus, composed of the stomach, liver, &c.; *d*, branchial lamina; *e*, the heart, from which proceeds the longitudinal trunk *f*, sending transverse branches across the body; *g*, *g*, projecting parts of the external tunic, serving to unite the different individuals into a chain.

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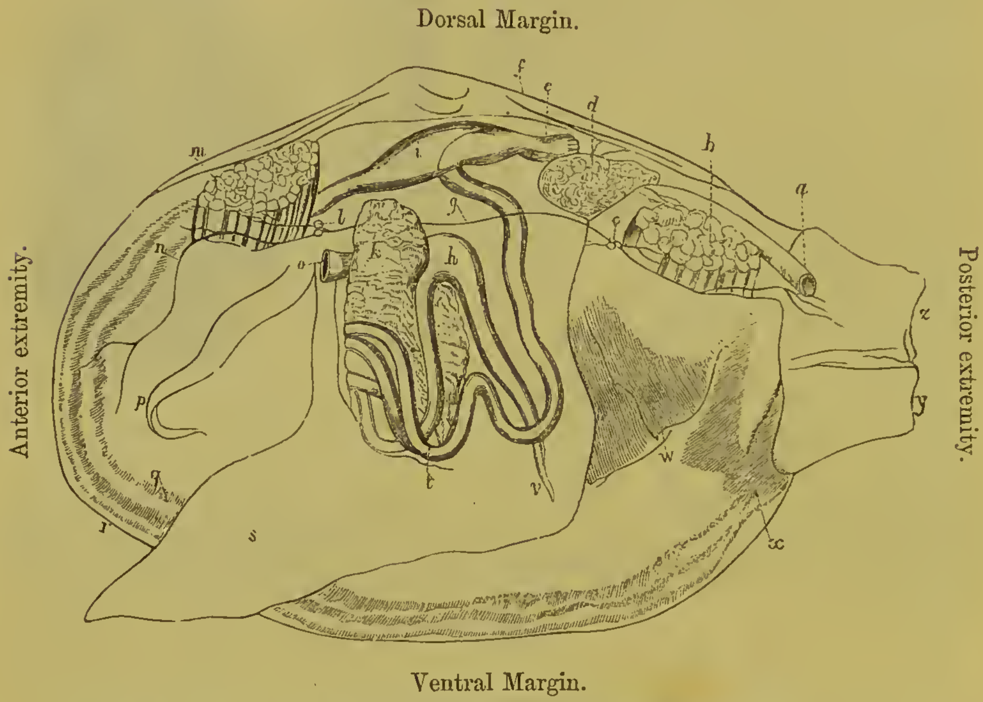
[*] See Mr. Huxley's admirable Memoir 'On the Morphology of the Cephalous Mollusca,' in the "Philos. Transact. 1852."

[†] Such is Mr. Huxley's very ingenious account of the production of this tunic, as given in his "Report on the Tunicata" to the British Association, 1852. See also his Memoirs 'On the Anatomy of Salpa and Pyrosoma,' and his 'Remarks upon Appendicularia and Doliolum,' in the "Philos. Transact." for 1851.

(here termed the *mantle*) being prolonged on either side into two lobes, which enwrap the body like a cloak, and form the valves of the shell upon their outer surface (Fig. 43). Again, a special development of muscular tissue in the integument of the 'ventral' or 'neural' region constitutes the 'foot' of those Lamellibranchiata which possess such an organ.—In the *Gasteropoda* this foot assumes the form of an expanded disk (Fig. 44, *a*), upon which the animal can crawl; the two extensions of the upper part of the integument are wanting; but the form of the body itself is entirely altered by the extraordinary and commonly unsymmetrical development of the hindmost portion of the hæmal region into a 'post-abdomen,' which contains the heart and a considerable part of the alimentary canal, and from the mantle of which a shell (Fig. 45) is very frequently produced. In the *pulmonated* Gasteropods (Fig. 124), however, the development takes place before instead of behind the anus; so that an 'abdomen' is formed instead of a post-abdomen.—This is also the case in the *Pteropoda*, in which the 'foot' proper is but little developed, whilst two lateral expansions (*epipodia*) sent off from it constitute the wing-like appendages (Fig. 46) from which the group receives its designation.—Finally in the *Cephalopoda*, the abdomen is so peculiarly developed that the alimentary canal is quite doubled upon itself, so as to bring the anus into immediate proximity with the mouth (as happens also in the *Bryozoa* at the opposite extremity of the series); the margins of the foot

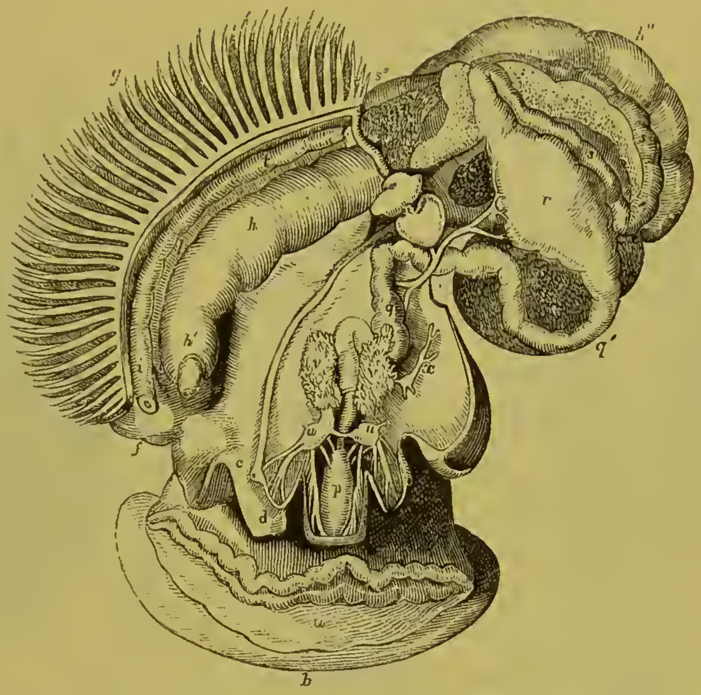
Fig. 43.



Anatomy of *Mactra*;—*a*, anus; *b*, posterior muscle; *c*, branchial ganglion; *d*, ovary; *e*, *t*, intestine; *f*, shell; *g*, nervous cord, connecting œsophageal and branchial ganglia; *h*, stomach; *i*, heart; *k*, liver; *l*, anterior or œsophageal ganglia; *m*, anterior adductor muscle; *n*, nervous filaments; *o*, mouth; *p*, one of the oral tentacula; *q x*, mantle; *r*, margin of the shell; *s*, foot; *w*, branchial lamellæ; *y*, oral siphon; *z*, anal siphon.

are prolonged into those prehensile processes (Fig. 47) which are termed 'arms;' and the posterior epipodial lobes, by their cohesion, form the

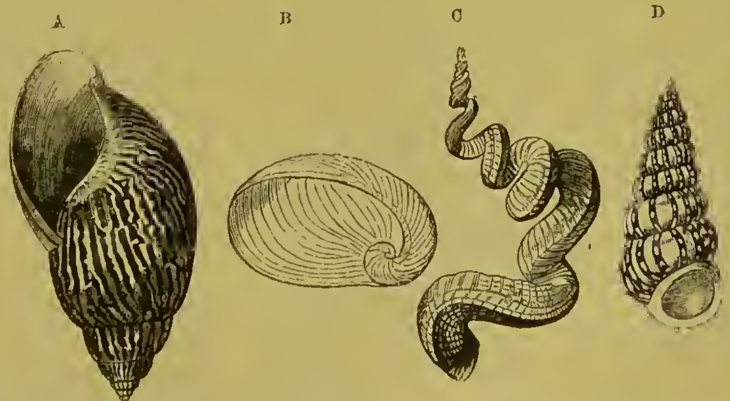
Fig. 44.



Paludina vivipara, withdrawn from its shell and laid open;—*a*, foot; *b*, operculum; *c*, one of the tentacula with its ocellus; *d*, siphon; *f*, border of the mantle; *g*, pectinated branchiæ; *h*, *h'*, the oviduct dilated for the retention of the ova; *h''*, portion of it situated within the spire of the shell; *i*, termination of the intestine; *l*, canal for the urinary (?) secretion; *n*, heart; *o*, liver; *p*, proboscis; *q*, *q'*, œsophagus; *r*, stomach; *s*, *s'*, *s''*, intestine, lying at *t* within the branchial cavity; *u*, *u*, cephalic ganglia; *v*, *v*, salivary glands; *x*, the principal muscular nerve.

funnel' that serves for the discharge of the respiratory current and of the matters ejected from the intestine.—Thus each of the subordinate types that we recognize in the Molluscous series, presents us with its own

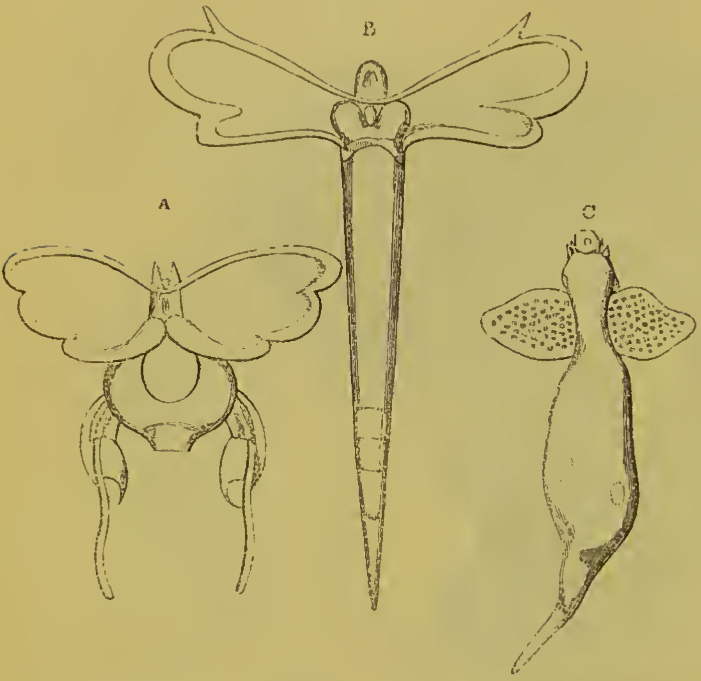
Fig. 45.



Shells of *Gasteropod Mollusks*:—A, Achatina;—B, Sigaretus;—C. Vermetus;—D, Scalaria.

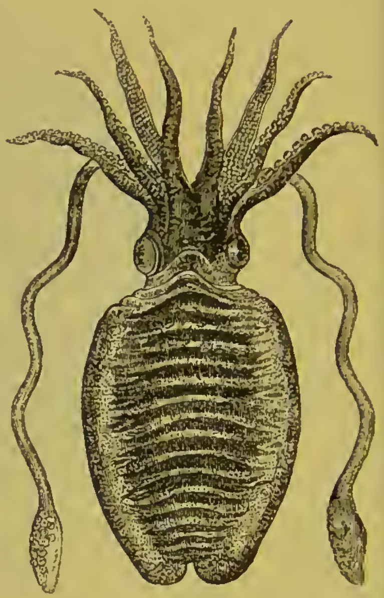
special character of differentiation from the general 'Archetype;' and there is no real transition from the one to the other.*

Fig. 46.



Existing forms of *Pteropods.*—A, Hyalæa; B, Criseis; C, Clio

Fig. 47.



Sepia officinalis, or Cuttle-fish.

42. Turning now to the internal organization of the animals of the Molluscous sub-kingdom, we find that the alimentary canal almost invariably presents a distinct separation between the œsophagus, the stomach, and the intestinal tube; this separation being as obvious in the zoophytoid *Laguncula* (Fig. 49), as in the Gasteropod *Aplysia* (Fig. 50). The mouth, or entrance to the œsophagus, is not situated, in the lower Mollusca, on a prominent part of the body, nor is it surrounded by organs of special

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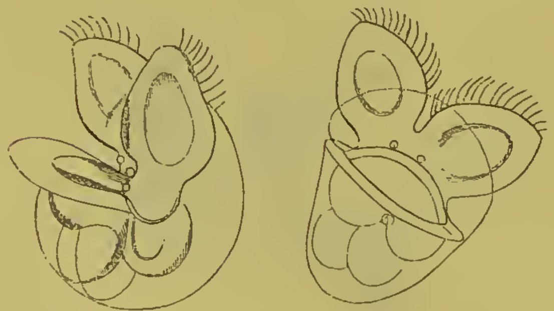
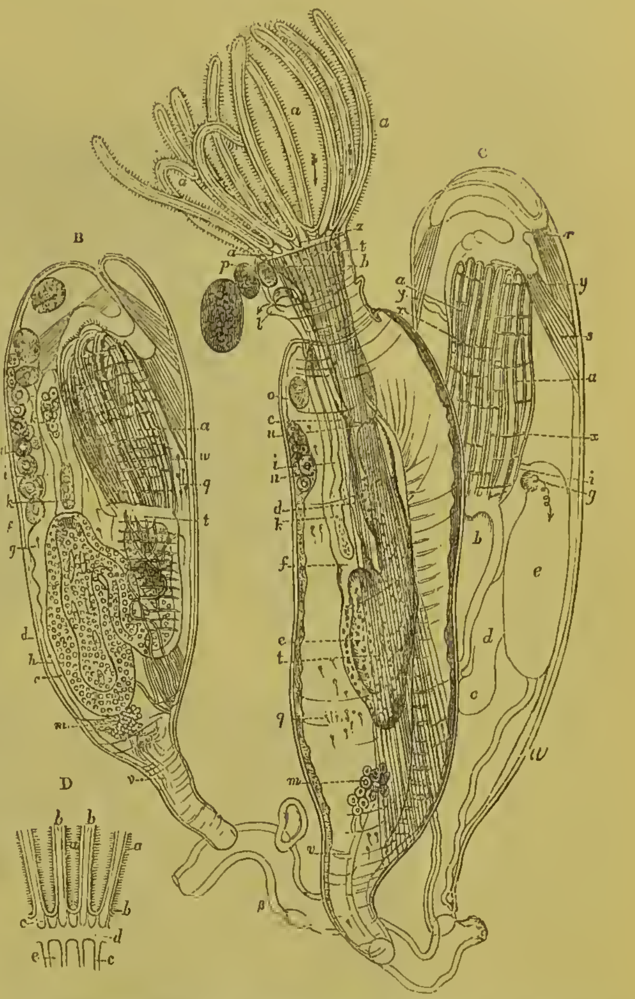
* When [it] was first discovered that the embryo-forms of Gasteropods (Fig. 48) possess a pair of ciliated lobes corresponding in general position with those of Pteropods, the notion was entertained by many, that the animals of the latter group must be considered in the light of permanent embryoes of the former: this, however, is inconsistent with the fact pointed out by Mr. Huxley, that the ciliated lobes of the embryo Gasteropods are homologous with the anterior portion of the epipodium, whilst it is the middle portion alone which is developed into the 'alæ' of Pteropods; and that a more fundamental distinction lies in the development of an 'abdomen' in Pteropods, whilst it is a 'post-abdomen' which is developed in Gasteropods.

Fig. 48.



Embryoes of *Nudibranchiate Gasteropods* sense; and hence these are distinguished as *acephalous.* In the higher classes, however, it is situated on a *head,* which projects from the trunk, and which is usually furnished with well-developed eyes, and with rudimentary organs of smell and hearing. In the lower Mollusca, again, there is a want of any prehensile or reducing apparatus, the food-particles being drawn-in by ciliary currents, which are also subservient to the respiratory function; but in the higher, the mouth is furnished with a complex apparatus for the reduction of solid food (Fig. 50, *a*), and prehensile instruments are added in the Pteropods and Cephalopods. In addition to this, a portion of the stomach is frequently developed into a gizzard-like structure, with very firm walls, adapted still further to crush and comminute the food; and this is found in many Bryozoa, as well as in several Gasteropods (Fig. 50, *i*) and in Cephalopods generally. The liver is always recognizably present; and although in the Bryozoa it consists of nothing else than an assemblage of isolated follicles, lodged in the walls of the stomach (Fig. 49, B, *h*), yet as we ascend the series, we find it gradually becoming more and more detached from that organ; and in the higher Mollusks it is developed into a compact viscus (Fig. 50, *l, l*), which frequently bears a very large proportion to the general mass of the body. As we ascend from the lower to the higher parts of the series, moreover,

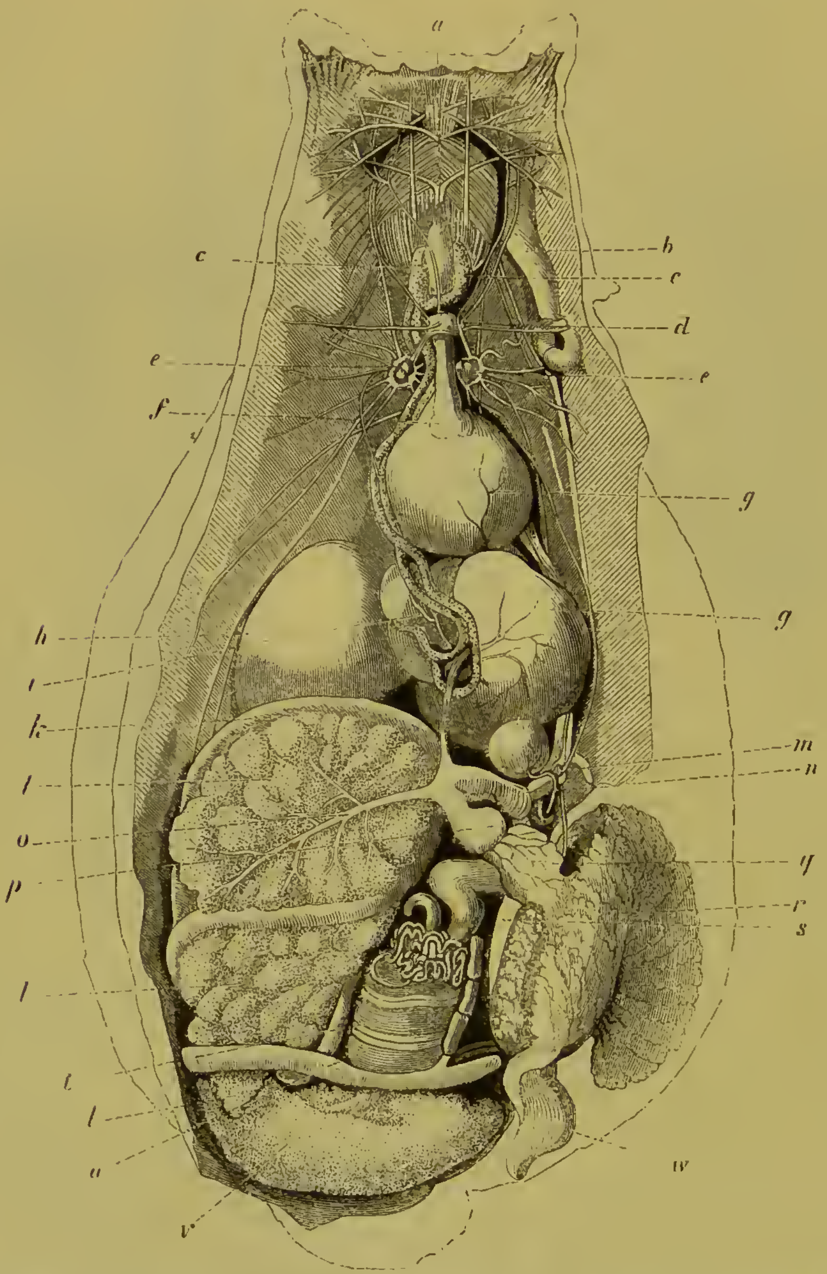
FIG. 49.



Laguncula repens, as seen in its expanded state at A, and in its contracted state, in two different aspects, at B and C. The same references answer for each figure:—*a a,* tentacula clothed with vibratile cilia; *b,* pharyngeal cavity; *c,* valve separating this cavity from *d* the œsophagus; *e,* the stomach, with *f* its pyloric valve, and *g* the circle of cilia surrounding that orifice; *h,* wall of the stomach with biliary follicles; *i,* the intestine, containing *k* excrementitious matter, and terminating at *l,* the anus; *m,* the testicle; *n,* the ovary; *o,* an ovum set free from the ovary; *p,* openings for the esape of the ova; *q,* spermatozoa freely moving in the cavity that surrounds the viscera; *r,* retractor muscle of the angle of the aperture of the sheath; *s,* retractor of the sheath; *t,* retractor of the tentacular circle; *u,* retractor of the œsophagus; *v,* retractor of the stomach; *w,* principal extensor muscle; *x,* transverse wrinkles of the sheath; *y,* fibres of the sheath, themselves probably muscular; *z,* muscles of the tentacula; α (at the base of the tentacular circle in A) nervous or œsophageal ganglion; *β,* stem.—D, a portion of the tentacular circle shown separately on a larger scale; *a a,* the tentacula clothed with cilia; *b b,* their internal canals; *c,* muscles of the tentacula; *d,* transverse muscles forming a ring at the base of the tentacula; *e,* muscles of the tentacular circle.

we find other secreting structures connected with the alimentary canal, such as the salivary glands and pancreas, presenting themselves in a more and more specialized condition; and the general type which these attain in Cephalopods, closely approximates to that under which we find them in Fishes. In no instance does the alimentary canal possess any direct

Fig. 50.



Aplysia laid open, to show the arrangement of the viscera :—*a*, upper part of the œsophagus ; *b*, penis ; *c*, *c*. salivary glands ; *d*, superior or cephalic ganglion ; *e*, *e*, inferior or subœsophageal ganglia ; *f*, entrance of the œsophagus into *g*, *g*, the first stomach or crop ; *h*, the third or true digestive stomach ; *i*, the second stomach or gizzard ; *k*, intestine ; *l*, *l*, *l*, liver ; *m*, posterior or branchial ganglion ; *n*, aorta ; *o*, hepatic artery ; *p*, ventricle of heart ; *q*, auricle ; *r*, *s*, branchiæ ; *t*, testis ; *u*, lower part of intestine ; *v*, ovary ; *w*, anus.

communication with the 'general cavity of the body,' in the midst of which it is suspended; but it may be affirmed with certainty that a transudation of nutritive material takes place through the walls of the former into the latter, and that this is the channel through which this material finds its way into the circulating system. For in the Bryozoa, there is absolutely no other means by which the body at large can be nourished, no true circulating apparatus existing in this group; so that the extension of the visceral cavity throughout the body, and even into the tentacula and stalk, constitutes the sole means by which the products of the digestive operation can be applied to the nutrition of the parts remote from the alimentary canal. Where a distinct vascular system exists, it communicates freely with this 'general cavity of the body;' so that the blood in one part of its circulation is freely discharged into it. In the higher Mollusks, however, the viscera themselves occupy so large a proportion of this cavity, that the remaining space is greatly reduced in size, and presents so much of the character of an ordinary venous sinus, that its true nature has not been until recently discovered. Notwithstanding this very important feature of degradation, we find the heart or central impelling organ of the circulation rapidly becoming more and more specialized as we ascend the series. No trace of it, of course, is to be found in the *Bryozoa;* in the *Tunicata* it is generally but little more than a pulsatile dilatation of one of the principal trunks (Fig. 42, *e*), the direction of whose action is not definitely settled; in the *Conchifera,* we first meet with a differentiation of auricle and ventricle; and this distinction becomes still more strongly marked, both structurally and physiologically, in the higher classes. With the exception of some of the lowest forms of the inferior types, we everywhere find a special provision for the aeration of the circulating fluid by means of a distinct respiratory apparatus; but the position of this varies more than that of any other organ in the body; and it is seldom that any other means are provided for renewing the water in contact with the respiratory surface, than the movement of the cilia with which it is clothed. No distinct urinary apparatus can be detected in the lower Mollusca; but its presence becomes distinctly recognizable in the higher.

43. Not only the Bryozoa, but by far the larger proportion of the proper Tunicata, possess a capability of multiplying by gemmation; the degree of connexion, however, that continues to exist between the gemmæ and the stock from which they have been put forth, varies in different groups. Thus in the Bryozoa a continuity is frequently preserved, as in *Laguncula* (Fig. 49), between the 'general cavity of the body' of one Zöoid* and another, through the whole of life; in *Perophora* (Fig. 138), the continuity is maintained by the vascular system, which is here in such free communication with the general cavity of the body that it may be almost regarded as a prolongation of it; in *Botryllus* (Fig. 51), the buds are formed in the first instance by an extension of the 'general cavity of the body' of the stock, but when they have attained an advanced stage of development they become entirely separated from it and from each other, although still enclosed within a common envelope;

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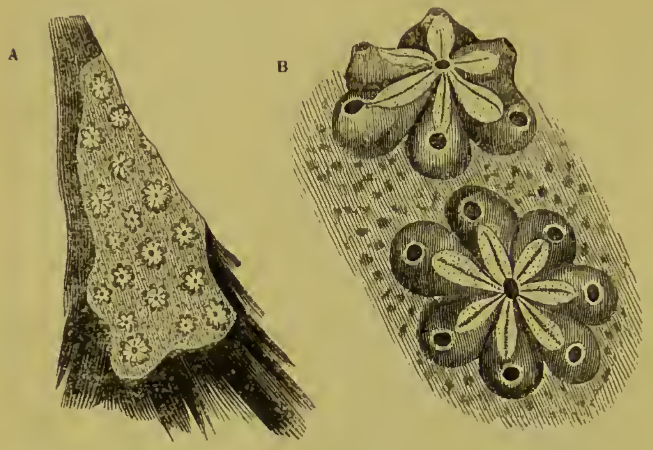
* The term *Zöoid* has been suggested by Mr. Huxley, as an appropriate designation for each of the independent and self-maintaining organisms, which collectively result from a single generative act.

and in *Salpa* (Fig. 42), the buds developed from the 'stolon' or creeping stem in the *interior* of the stock, become detached at a very early period, and swim forth freely, although connected into chains by the mutual adhesion of their bodies. No multiplication by gemmation is known to exist in any of the higher Mollusca; but a peculiar generative zöoid is detached from the male of certain Cephalopods, to convey to the female his spermatic fluid.—The true generative apparatus is very distinctly evolved throughout the series. In its lowest classes, the two sets of organs are united in the same individual, in such a manner that its 'sperm-cells' may impregnate its 'germ-cells,' and thus produce fertile ova, without any special operation. In certain of the Bivalves, however, the sexes are distinct; but the fertilization of the ova is provided-for without any special congress of two individuals. In the Pulmonated Gasteropods both sets of organs are present in each individual, but they are not usually self-impregnating; for the generative act is ordinarily effected by the congress of two individuals, each fertilizing the ova of the other by means of a highly-developed intromittent apparatus. In all the other Cephalous Mollusca, the sexes are distinct; and a regular sexual congress usually takes place.

FIG. 51.



Botryllus violaceus:—A, cluster on the surface of a Fucus:—B, portion of the same enlarged.

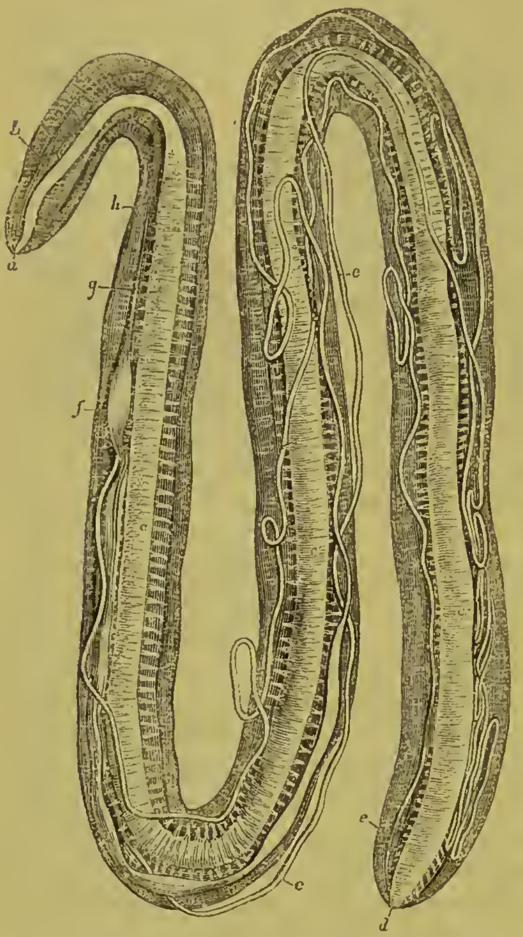
44. No part of the organization of Molluscous animals exhibits the principle of differentiation more remarkably, than does the Nervous system. For whilst, in the Bryozoa and Tunicata, we find it to possess but a single ganglionic centre, which answers all the purposes required by the low development of their animal functions, a progressive multiplication of ganglionic centres manifests itself as we ascend the series; this multiplication not being dependent, as in Radiata and Articulata, upon the repetition of similar ganglia (save in certain special cases), but having reference to the greater variety of purposes which this system is called-on to effect, chiefly in virtue of the development of more special organs of sensation and motion. In the Acephalous Mollusks, there is an almost entire absence of visual organs, and no trace of auditory or olfactive; and the movements of such of them as are not fixed to one spot, are of the simplest and least varied nature, being effected either by the agency of the ciliary currents, or by general contractions of the muscular sac, or (in the Bivalves) by the contraction of those special collections of muscular fibres, which constitute the adductor muscles and foot. In the Cephalous Mollusks, the rudimentary eyes found in some Acephala are progressively developed into organs fitted for distinct vision; rudimentary organs of hearing begin to show themselves, which are evolved among Cephalopods into a proper auditory

apparatus; indications of a specialization of a part of the surface for olfactive purposes are also perceptible; and conjointly with this advance in the sensorial apparatus, we find the capacity for locomotion,—which is so feeble in most of the Gasteropods, that the term 'sluggish' derived from one of the best known members of that class is applicable to the whole of it,—greatly augmented in the Pteropoda and Cephalopoda, many of the latter being nearly as active as Fish.

45. The plan of construction presented to us in the assemblage of animals constituting the sub-kingdom ARTICULATA, is much more definite than that which we have traced through the Molluscous series; and its leading features are in general more easily recognized, since the departures from the 'archetype' form are seldom such as to interfere with the manifestation of its fundamental idea. Thus even in the *Cirrhipeds* (Figs. 4, 5), which constitute its most aberrant group, the *Molluscoid* characters are superficial only, whilst the prevalence of the Articulated type through every part of the internal organization is at once revealed by anatomical research.—The body of every Articulated animal is composed of a succession of *segments* arranged longitudinally; the division being usually indicated externally by a differentiation in the consistence of the tegumentary skeleton, and by the repetition of the appendages (where such exist) which each segment bears. There is a manifest predominance, in the greater part of the series, of the organs of *animal* life over those of organic or *vegetative* life; for the apparatus which is subservient to the locomotive powers, occupies, in all the higher Articulata, a very prominent position; and it is kept in a state of high activity under the guidance of senses of remarkable acuteness. As it is by the external skeleton alone, that fixed points can be afforded for the attachment of the muscles and for the fulcra of the levers by which motion is given to the body, the degree of its consolidation generally corresponds with the development of the locomotive apparatus; the chief exceptions being presented by those cases in which (as in the common Crab) there is an extraordinary development of a solid *test* for the purpose of protection only.—In some of the lowest grades of this type (belonging to the group of Entozoa), the successive segments which are indicated externally by constrictions of the body, so exactly repeat each other, that each can maintain an independent existence, and can reproduce the entire body by gemmation; so that, being indefinite in number, and physiologically distinct, they are nearly on the same footing with the independent zöoids of a Botryllus. It is interesting to remark, moreover, that among these the Molluscous nature so far predominates, that there is scarcely a trace of locomotive organs, and the integument is soft throughout, so that the segmental division is chiefly indicated by the repetition of the organs of nutrition and reproduction. Ascending to the Nematoid Worms (Fig. 52), we find the segments united into one continuous body, not only externally but internally; and in these we find some of the leading features of the Articulated type displayed in their simplest condition. The body does not externally present any true annulations, but a transverse wrinkling of the integument is generally perceptible; and the muscular fibres which line this integument are disposed in regular transverse bands, which are often sufficiently developed to endow these animals with a power of active movement. The oral orifice (*a*), situated at one extremity of the body, leads to an

alimentary canal (*c,c,c*), which runs through the axis of the cylinder to the anal aperture (*d*) at its opposite extremity; presenting in its course scarcely any differentiation of parts into œsophagus, stomach, or intestine, and no distinct glandular appendages. There are two pairs of longitudinal vessels, one of which is supposed to be arterial and the other venous; but there are not yet any special respiratory organs, the low degree of aeration which their circulating fluid requires, being still attained through the intermediation of the soft integument. The nervous system chiefly consists of a pair of longitudinal trunks which run along the ventral region of the body, and are connected with a pair of very minute ganglia on each side of the œsophagus; but no distinct ganglionic enlargements present themselves in the course of these trunks; nor is there the least indication of the presence of organs of special sense. The two sexual divisions of the generative apparatus, which are not only combined in the lower Entozoa in the same individuals, but are even repeated through their successive segments, are here assigned to distinct individuals; and the form alike of the ovary (*e, e, e*) and testes usually participates in the general elongation, which may be considered as resulting (like that of the digestive and vascular apparatus) from the 'fusion' of the parts proper to each segment.—Hence the differentiation of parts is here almost at its minimum; for there is nothing that can be properly termed a head; and with the exception of the two terminal segments and that which contains the genital orifice, there is scarcely one that differs from its fellows in any essential particular of external configuration or internal structure.

FIG. 52.

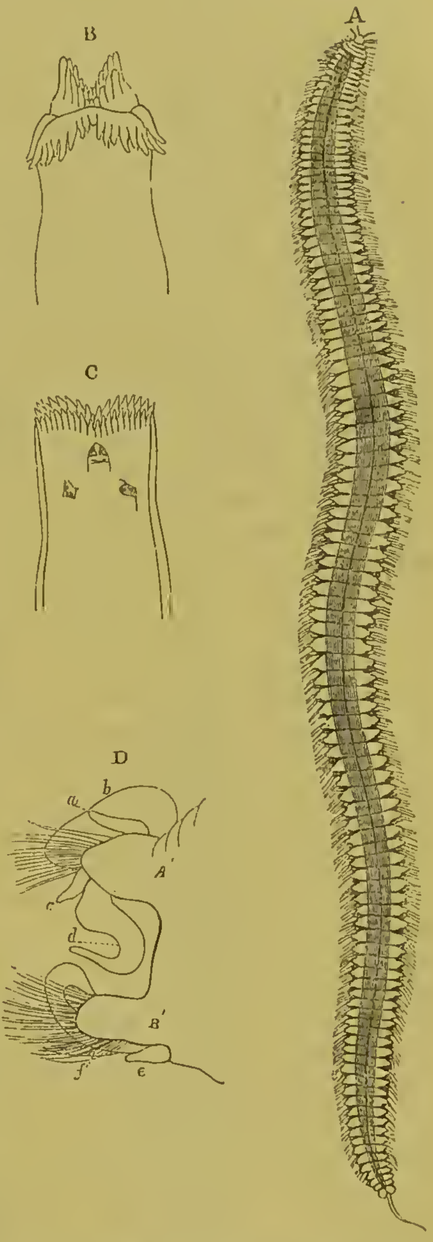


Strongylus gigas (female) laid open to show its internal structure;—*a*, mouth; *b*, œsophagus; *c, c, c*, intestinal canal; *d*, anus; *e, e, e*, ovary; *f*, uterine dilatation; *g*, narrow oviduct; *h*, its orifice.

46. In the class of *Annelida* we meet with a decided advance in the degree of specialization of the several organs, both of Animal and of Vegetative life, without, as yet, any marked differentiation of the regions of the body, which is usually composed of a large number of segments presenting a close external resemblance (Fig. 53, A). In the lower forms, which nearly approximate to the higher Entozoa, the segmental division is obscured by the general softness of the integument, and by the absence

of locomotive or branchial appendages; but in proportion as these are developed, and as the integument becomes consolidated, the *annulose* character is made obvious, by the alternation of firm rings with soft intervening membrane. So, again, in the lower forms of this group, the head is scarcely more differentiated from the body than it is in the Nematoid Entozoa; whilst in the higher, it is furnished with proper eyes and antennæ, and the mouth is provided with an elaborate apparatus, consisting either of one, two, or three pairs of jaws, or of an evertible proboscis, for the prehension and reduction of food (Fig. 53, B, C). Where locomotive appendages are developed, as in the tribe of *Nereids*, they are almost precisely repeated from one end of the body to the other; and this is the case, also, with the respiratory organs, save where the conditions of existence require that these should be especially developed from some particular region, as is the case with the cephalic branchial tufts of the *Sabella* (Fig. 144); in fact, the respiratory and locomotive organs in this group are by no means completely differentiated from one another, each being subservient in greater or less degree to both purposes. These appendages vary in different genera; but we usually find them based on two fleshy tubercles on either side of each segment, which are termed the 'dorsal oars' (Fig. 53, D, A′), or the 'ventral oars' (B′), according as they project from the upper or under half of the segment. Each oar commonly possesses, attached to the base of its tubercle, a long soft cylindrical appendage, or *cirrhus* (D, *a*, *e*), homologous with the anteniform appendages of the cephalic segment; whilst its summit bears a tuft of *setæ* or bristles, which serve as the instruments of locomotion when the animal is crawling over solid surfaces. In the ordinary Nereids, moreover, each oar has also a membranous lobe (D, *b*, *f*), which is its instrument of propulsion in water. All these appendages, together with the pre-

Fig. 53.



A, *Nephthys Hombergii*; B, its proboscis; C, the same laid open, to show the horny teeth it contains; D, one of the feet, showing A′, dorsal oar; B′, ventral oar; *a*, dorsal cirrhus; *b*, membranous lobe of dorsal oar; *c*, tentaculiform appendage; *d*, branchial appendage; *e*, ventral cirrhus; *f*, membranous lobe of ventral oar.

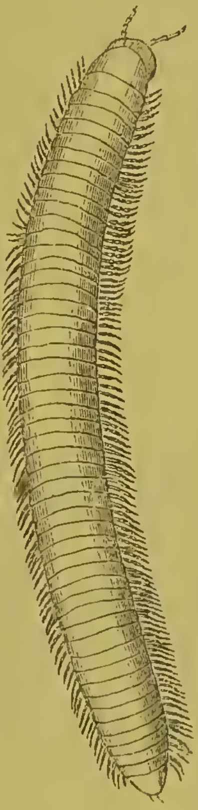
hensile and tactile organs which are developed around the mouth of many species, are probably subservient in greater or less degree to the aeration of the nutritive fluid transmitted to them; but a more special respiratory organ (*d*), consisting either of a flattened vesicle or of a branching tuft, is developed from the under side of the dorsal oar; this is not usually repeated, however, through the entire length of the body.

47. Notwithstanding the elaborateness of the buccal apparatus, the alimentary canal still retains much of its primitive simplicity, being an almost straight tube without any obvious division into œsophagus, stomach, and intestine; it is, however, furnished with cæcal appendages of various kinds, apparently of a glandular character. The condition of the sanguiferous system in this group is very peculiar; for whilst in the higher Articulata, as in the Mollusca, it communicates freely with the general cavity of the body, so that one and the same fluid circulates through both, the blood-vessels here form a completely *closed* circuit, as in the Echinodermata; and the general cavity is occupied by a true 'chylaqueous' fluid, which is kept in pretty constant motion by the movements of the body. As in the Echinodermata, too, there appear to be distinct provisions for the aeration of the blood-proper and for that of the chylaqueous fluid; for whilst the latter penetrates into the locomotive, prehensile, and tactile appendages, and is freely exposed through their parietes to the surrounding medium, it is the blood alone which is transmitted to the special respiratory organs. The generative apparatus in the Nereids, as in the Cestoïd Entozoa, is completely repeated in each successive segment; but in the *Terricolæ* (Earth-worms, &c.) it is more localized, having only a single external orifice, as in the Nematoid worms; and although both male and female organs are developed in the same individual, yet the congress of two is necessary, as in the terrestrial Gasteropods, each impregnating the other. The multiplication of parts by gemmation takes place to a great extent among the Annelida; for it is in this way that the extraordinary elongation of the body is effected, which is characteristic of many species; the number of segments being thus augmented, from the single one which presents itself in the earliest stage of development, to four or five hundred. And there are certain species in which the body spontaneously divides itself into parts, each of which becomes a complete organism; whilst in others, portions of the body endowed with locomotive and sensory organs, but unprovided with a nutritive apparatus, are budded-off, for the purpose of dispersing the products of the generative act, with which they are loaded. The nervous system here presents a far higher development than in the Nematoidea, as might be expected from the presence of distinct organs of sense, and of locomotive appendages; for the double ventral cord is now studded with ganglia, disposed at regular intervals, and equal in size, thus conforming to the general similarity of the segments themselves; whilst the cephalic ganglia exceed the rest in size, and acquire a directing power over them, in a degree proportionate to the development of the organs of special sense.—It is worthy of note, that even in this group, which, as a whole, is characterized by its locomotive activity, there is an entire order adapted to lead the sedentary life of Molluscous animals; some of them even forming shelly tubes, which can scarcely be distinguished from those of certain Gasteropods. Various modifications of

structure are required for this purpose, especially the concentration of the respiratory apparatus about the head; but it is to be remarked, that these special modifications begin to make their appearance at an advanced stage of development,—these *Tubicolæ,* up to a certain point, not only leading the errant lives of the Nereids, but exhibiting an almost exact conformity to *their* type of conformation.

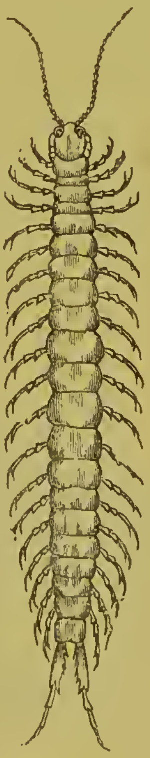
48. Disregarding the more aberrant forms of the Articulated sub-kingdom, and restricting ourselves to that tolerably regular series which will best illustrate the principle of progressive differentiation, we now come to the class *Myriapoda,* in which we find the *regular* evolution of this type attaining its maximum. The segmentation of the body in this class is rendered very distinct, by the hardening of the integument of its successive divisions, and by the interposition of a flexible membrane between each pair, so as to allow of considerable freedom of motion; and the same kind of articulation is presented also by the locomotive appendages. These in the *Iulus* (Fig. 54) are very numerous, like the segments to which they are attached, but are very imperfectly developed, showing only a slight advance upon the ventral setæ of the Nereids, which they may be considered to represent; so that the animal seems rather to glide or crawl with their assistance, like a Serpent or Worm, than to rely on them for support and propulsion. The case is different, however, with the *Scolopendra* (Fig. 55); for here the number of segments is

FIG. 54.



Iulus.

FIG. 55.



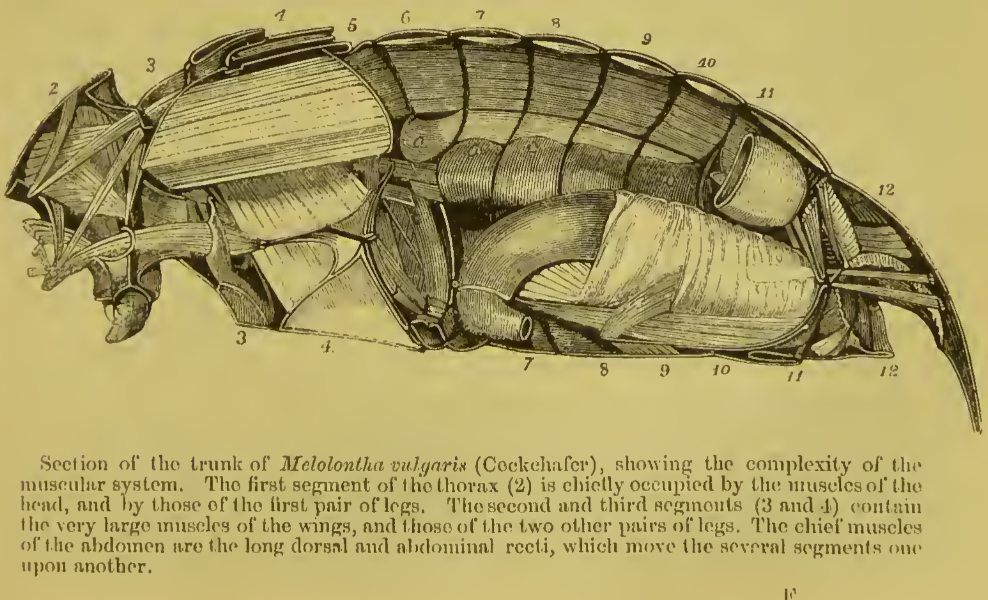
Scolopendra.

greatly reduced, whilst each attains a higher grade of development, especially as regards its locomotive appendages and the muscles by which they are put in action. Still we observe as complete an outward equality in the successive segments, as the Annelida present; it being the head alone which presents a marked differentiation in the *Iulidæ;* whilst the appendages of the first segment of the body in the *Scolopendridæ,* instead of being employed for locomotion, are so modified as to serve to hold and tear their prey, and are also provided with an apparatus for instilling poison into the wounds they make.—The alimentary canal of the Myriapods for the most part exhibits a division into œsophagus, stomach, and intestine, the stomach usually possessing distinct muscular walls, and being sometimes lined with a plaited horny membrane, so as to constitute a kind of gizzard; and long tubular cæca are connected with various parts of this canal, which probably act as salivary, hepatic, and urinary glands. The long vascular trunk, or 'dorsal vessel,' exhibits a regular segmental division, each portion being in fact the impelling cavity or heart of the segment in which it lies, whilst there is such a communication between the several chambers, that a general movement of the blood from behind forwards can take place through the trunk formed by their union. The venous circulation, as in Insects, Crustacea, and Arachnida, is carried on through the general cavity of the body and the interstitial lacunæ in the members. The respiratory organs, which are here internal, are repeated with almost perfect uniformity through the entire series of segments; each having its pair of *stigmata* or breathing pores, which lead either to simple air-sacs, or to branching tracheæ. Both in *Iulidæ* and *Scolopendridæ,* the sexes are distinct; but the generative apparatus of each sex is still extended through a considerable part of the body, although it has but a single external orifice. In the development of the organism, we still witness a multiplication of segments by gemmation; one after another being produced, subsequently to the young Myriapod's emersion from the egg, until the number proper to the species is attained. The nervous system is formed upon precisely the same general plan as that of the Annelida; the ventral ganglia, however, being considerably larger in proportion, in accordance with the higher development of the locomotive apparatus; whilst the cephalic ganglia also show a great increase, in accordance with the increased elaborateness of the sensory organs. We now find, moreover, a special division of the nervous system, appropriated to the respiratory apparatus, its ganglia being repeated, like the organs it supplies, in each segment; and a like special arrangement of ganglia and nerves (of which traces are discoverable among the Annelida) is provided for the supply of the buccal apparatus and stomach, and is hence termed the 'stomato-gastric' system.—Thus we see that in this interesting group of animals, which exhibits in its general organization the greatest elaborateness that is compatible with the external maintenance of the uniform Articulate type, a certain amount of differentiation has already begun to show itself in the disposition of the internal organs.

49. This differentiation is carried to a far higher extent, however, in the class of *Insects;* in which segmental uniformity is completely sacrificed, for the attainment of the special objects contemplated in the organization of this type. In many larvæ, it is true, that uniformity is as perfect as in the Nematoid Worm or the Nereid; but in the course of

that development which is known by the term *metamorphosis*, both the external configuration and the internal structure of the several segments become more and more diversified; and at last we find the entire body separated by well-marked divisions into head, thorax, and abdomen, the thorax being always composed of three segments, and the abdomen of nine, unless one or two of the terminal segments should have been suppressed. Now although all these segments, in the larva state, may have been equally provided with locomotive appendages, or may (on the other hand) have been entirely destitute of them, we find that, in the perfect Insect or *imago*, only the three thoracic segments are thus endowed; this limitation of the motor organs, however, being accompanied with a much higher development of the members themselves. Each of the three thoracic segments is provided with a pair of articulated legs; and whilst in the Myriapoda the successive joints were almost exact repetitions of each other, we now distinguish the diversely-formed parts which are known as the *coxa* or 'hip', the *femur* or 'thigh', the *tibia* or 'shank', and the *tarsus* or 'foot',—names which, suggested by the analogy of animals constructed upon a plan essentially different, are by no means strictly applicable. But besides these members, which may be considered as homologous with the cirrhi of the 'ventral oars' of the Nereids (Fig. 53, D, *e*), the second and third segments of the thorax are each furnished (in the typical Insect) with a pair of wings, which may be likened to the membranous lobes of the 'dorsal oars' (*b*), being expansions of the outer tegumentary membrane over a frame-work supplied by the dermal skeleton. This skeleton often undergoes very remarkable modifications; one piece (usually the first segment) being sometimes enormously developed at the expense of the other two, so as even entirely to conceal them on the dorsal surface; whilst in other instances a partial or complete adhesion takes place between the several rings. In either case, a degree of consolidation of the thoracic segments is afforded, which, whilst entirely

FIG. 56.



Section of the trunk of *Melolontha vulgaris* (Cockchafer), showing the complexity of the muscular system. The first segment of the thorax (2) is chiefly occupied by the muscles of the head, and by those of the first pair of legs. The second and third segments (3 and 4) contain the very large muscles of the wings, and those of the two other pairs of legs. The chief muscles of the abdomen are the long dorsal and abdominal recti, which move the several segments one upon another.

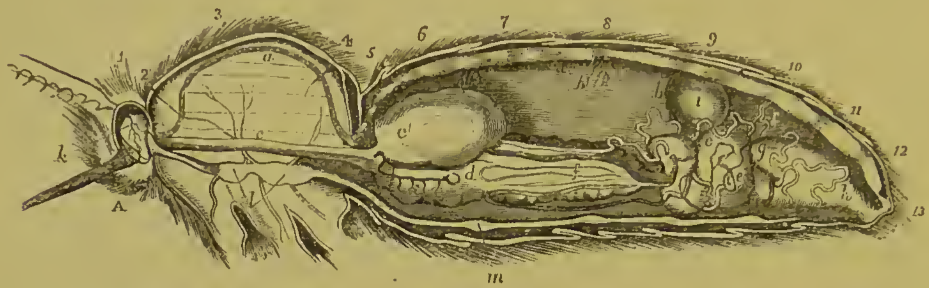
destroying their mobility one upon the other, gives a far more secure attachment to the complex assemblage of muscles (occupying almost the whole interior of the thorax, Fig. 56) provided for the movement of the legs and wings, to which the locomotive function is now delegated. The abdominal segments, however, for the most part preserve their primitive ring-like simplicity, and are put in motion, one upon another, by longitudinal and transverse muscles that differ little from those common to Articulata generally; but the abdomen also contains special groups of muscles, developed in connection with organs peculiar to certain tribes of Insects, as stings, ovipositors, &c. All this differentiation of the muscular system takes place gradually, like the evolution of the organs to which the several groups of muscles are subservient.

50. The head of the Insect is not only more completely separated from the trunk than it is in any other Articulated animals, so as to be endowed with greater freedom of motion; but it is also provided with a far more elaborate apparatus for sensation. Thus the organs of vision appear to be no less efficient in guiding the movements of these animals, than are the most perfect eyes of Vertebrata, although constructed upon a very different type: for in the place of a single movable eye on each side of the head, we find an assemblage of cylindrical or conical *ocelli*, sometimes to the number of several thousand, each of them adapted to receive rays in one direction only. This arrangement is common to the whole Articulated series, with the exception of the Arachnida, and is conformable to that general plan of repetition of similar parts, of which we have seen so many examples in them; but it is in Insects that we find the ocelli most numerous, and their structure most complete. The organs of touch are also multiplied; for besides the *antennæ*, which serve by their elongation (which is frequently most extraordinary) to take cognizance of objects at some distance, we find two pairs of short *palpi*, whose special function it seems to be to examine substances in the immediate neighbourhood of the mouth; and there is reason to believe that one or both of them are specially endowed as instruments of smell. It is certain, too, that there is some provision for the sense of hearing; although its special instrument has not yet been positively made out. The nervous centres, with which locomotive and sensory organs are in connection, exhibit very marked characters of differentiation, in accordance with the foregoing special developments. Thus whilst in the Larva, the ganglia of the successive segments correspond in size, and are disposed at equal distances from each other, we find in the Imago an extraordinary development of the thoracic centres (Fig. 57, *l*), which, being also approximated more closely, sometimes even run together into a single ganglionic mass; whilst some of the abdominal ganglia (*m*) almost disappear, and their distance remains undiminished. So, again, the cephalic ganglia (*k*), which in the Larva (as in the lower Annelida) scarcely surpass the ventral ganglia in size, attain an enormously-increased development in the Imago; this being obviously related in great part to the perfection and activity of the visual organs, by whose agency the movements of these animals are guided.

51. In the structure of the Nutritive apparatus, and especially of the Digestive system, the principle of differentiation is very strongly marked; and this, not only in the type common to the class taken as a whole, but also in the subordinate modifications which its various subdivisions pre-

sent, adapted as they are to exist upon the most diverse kinds of nutriment. The buccal apparatus presents two principal forms, one constructed for mastication (as is characteristically seen in the Beetle tribe), the other for suction (of which the Butterflies, &c. present the best examples); yet although these forms are subject to almost endless modifications, the same elementary parts may be everywhere traced, thus showing a most remarkable example of 'unity of type.' The alimentary canal always exhibits a well marked distinction into œsophagus, stomach, and intestine (*c*, *d*, *e*); and the stomach is frequently furnished with an apparatus suited for the mechanical reduction of the food. The glandular appendages are usually more highly developed in this class, though still preserving a very simple type, so that their character is chiefly determined by the part of the canal into which they discharge their product. The circulating apparatus is formed upon the incomplete type already noticed in the Myriapoda; for its centre consists of a many-chambered dorsal vessel (*a*, *a*), from which arterial trunks proceed to the system generally; whilst the return of the blood takes place through the general cavity of the body, the insterstitial lacunæ between the muscles, &c. Some differentiation is observable, however, even here; for whilst in the larva, as in the lower Articulata, the chambers of the dorsal vessel correspond in number and position with the segments of the body, their number is reduced in the perfect Insect, by the contraction of the thoracic chambers into a mere arterial trunk, whilst those of the abdomen are enlarged and become more muscular; and although each of the latter continues to act as the heart of its own segment, yet by their successive contractions from behind forwards, they propel a more vigorous current towards the anterior part of the body. The respiratory apparatus of Insects is very greatly extended, the tracheæ being prolonged into every part of the body; in its grade of development, however, no decided advance is made upon the type of the Myriapoda; although indications of differentiation are seen in the closure of the spiracles of certain segments, whilst those of other segments are enlarged, so that the whole apparatus is supplied with air through a comparatively small number of openings.—The reproduction of Insects, with only one known exception, is accomplished solely by the true generative process. The sexes are distinct throughout the class; and the males and females are frequently distinguished by diversities in size, configuration, or colour, as well as by the difference in their generative organs. The seminiferous or oviferous tubes possess but a single outlet, although they are frequently greatly multiplied, or, if few in number, are extended through a large part of the body; and the last segment of the abdomen is usually adapted in the male to serve as a penis or intromittent organ, whilst in the female it is developed into an ovipositor. In the exception above alluded to, that of the *Aphides*, a succession of 'zooids' is produced, without any sexual intervention, by a process which seems to be essentially one of internal gemmation. No multiplication of segments by gemmation ever seems to occur in this class; the embryo, when first its outlines can be discerned, presenting the full number. It seems obvious, then, that the productive energy is here expended, not upon the 'vegetative repetition' of similar parts, but upon that higher development of a smaller number, which renders them capable of a far greater variety, as well as of greater energy, of functional power.—The general arrangement of the Nutritive organs in this class, is shown in the accompanying section of a Lepidopterous insect. As compared with Vertebrata, the whole body may be considered as inverted; the ganglionic column which answers to the spinal cord being situated on the ventral aspect; whilst the central organ of the circulation is on the dorsal.

Fig. 57.

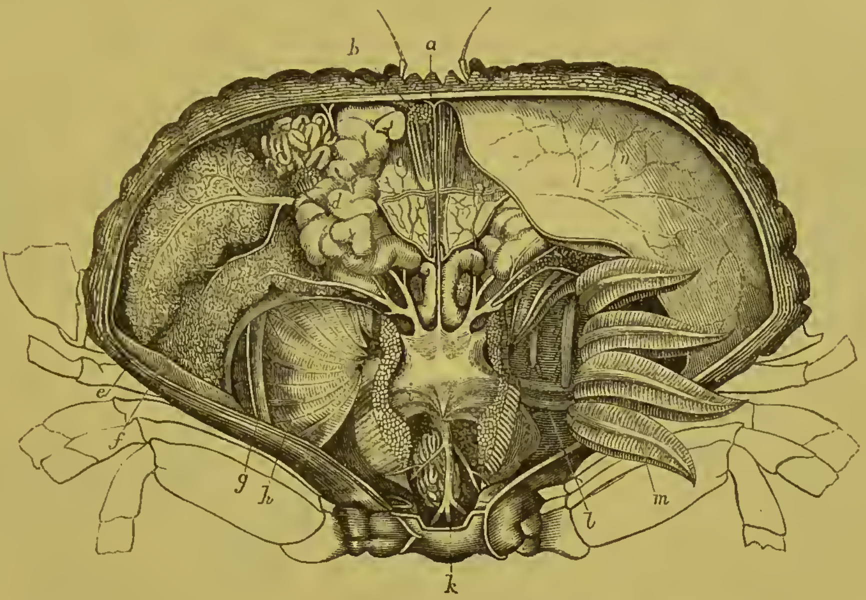


Ideal Section of *Sphinx ligustri* (Privet Hawk-moth), to show the relative position of its organs;—1—13, successive segments; *a, a,* dorsal vessel; *b,* ligamentous bands holding it in place: *c,* œsophagus; *c′,* crop; *d,* stomach; *e, e,* intestinal canal; *f, f,* biliary tubuli; *g,* cæcum; *h,* cloaca; *i,* ovary; *k,* cephalic ganglia; *l,* thoracic ganglia; *m,* first abdominal ganglion.

52. A very analogous description might be given of the class of *Crustacea,* in which we find the higher type of articulated structure modified for inhabiting water; but it will be sufficient for our present purpose to notice some of the most striking contrasts which it presents between the lowest and the highest degrees of differentiation. Among some of the *Isopod* Crustacea, there is as complete an equality between the different segments, as there is in the Myriapoda; whilst in the *Brachyourous Decapods* (Crab tribe) there is a most remarkable differentiation, the segments of the cephalo-thorax being immensely enlarged, and fused (as it were) together, whilst those of the abdomen are scarcely at all developed, and the whole being covered-in by a *carapace* formed by an extraordinary backward extension of one of the cephalic rings. The same kind of alteration extends to the internal organs; for everywhere we notice a remarkable fusion and concentration of what are elsewhere separate parts. Thus of the dorsal vessel, only a single chamber is developed into a heart, but this attains a very large size (Fig. 58, *i*), and has powerful muscular walls, whilst the anterior and posterior portions dwindle-down into arterial trunks (*a*, *k*). The nervous system exhibits a like concentration; all the ganglionic centres proper to the thoracico-abdominal segments being fused into one mass, from which nerves radiate to the limbs and to the rudimentary abdomen. It is not in this manner alone, however, that the ordinary articulated type undergoes modification in the higher Crustacea; for we find the liver (*e*), formed rather upon the plan of Mollusks than upon that of Insects, being a compact organ, composed of multitudes of short follicles crowded upon excretory ducts like grapes upon a stalk; and this peculiarity extends to other glandular organs, as also to the generative. All these modifications are of special interest, when taken in connection with the

aquatic respiration and comparatively inert habits of these Crustacea, which mark their differentiation from the ever-active aerial Insects, as being

Fig. 58.



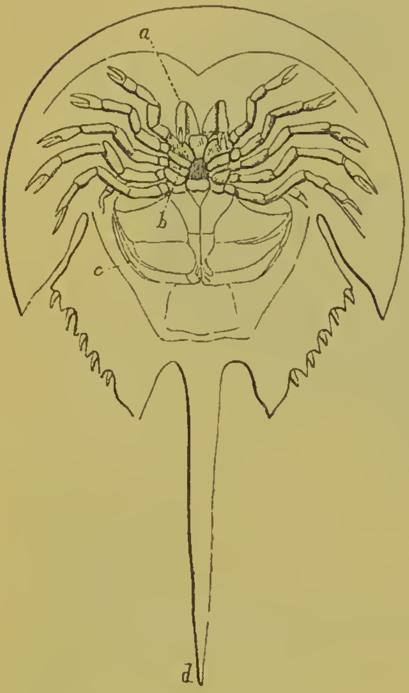
Anatomy of *Cancer pagurus* (Common Crab), the greater part of the carapace having been removed;—*a*, ophthalmic artery; *b*, muscles of the stomach; *c*, stomach; *d*, intestine; *e*, liver; *f*, testis; *g*, flabella; *h*, branchiæ in their normal position; *i*, heart; *k*, abdominal artery; *l*, vault of the flank, enclosing the branchial cavity; *m*, branchiæ turned back.

(so to speak) in the Molluscan direction. It is peculiarly interesting to observe, that this extreme departure from the 'archetype' conformation only arises gradually; the young Crab, soon after its emersion from the egg, resembling the young of many long-tailed Crustacea; and the extraordinary development of the cephalo-thorax, with other specialities of structure, being only attained after a succession of changes that may be considered as amounting to a metamorphosis (Fig. 77).

53. Although a powerful masticatory apparatus is usually provided in the higher forms of this class, consisting of several pairs of jaws opening laterally, yet these jaws, which stand in the same relation to the cephalic segments that the legs do to the thoracic, are not completely differentiated from the locomotive apparatus: the three pairs which are posterior to the mouth presenting a gradual approximation to the anterior pairs of thoracic members, so as to be actually employed in the Stomapods for prehension and locomotion, whilst in the Decapods the anterior thoracic members are converted into supplementary feet-jaws; so that a regular gradation is established between the typical mandibles in front of the mouth, and the typical legs belonging to the posterior segments of the thorax. Now in the curious *Limulus* (king-crab), which forms a connecting link between the higher Crustacea and the inferior group of Entomostraca, the two functions of mastication and locomotion are actually performed by the same members; for the ordinary cephalic instruments of mastication are wanting, and the thoracic limbs are so arranged round the mouth, that their basal joints may work against

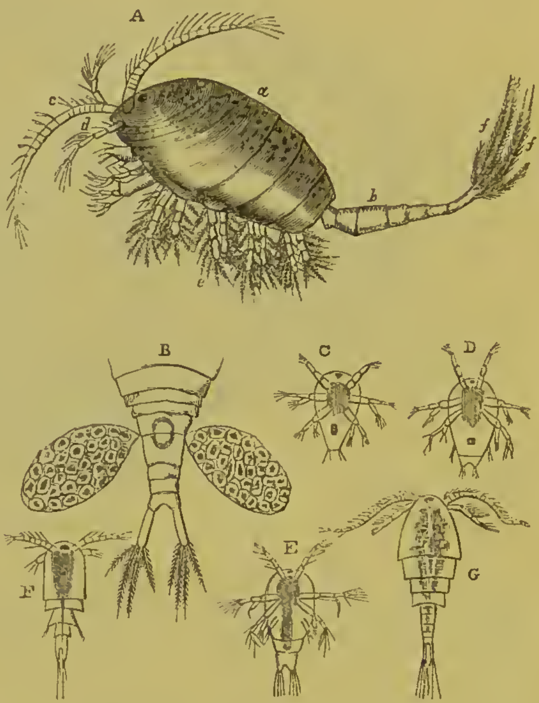
those of the opposite side, and may thus serve as jaws, whilst the remainder of each member acts as an ordinary instrument of locomotion and prehension (Fig. 59). In the *Entomostraca*, again, we find the organs of respiration very imperfectly differentiated from those of locomotion; some of the group being furnished with 'fin-feet,' which are obviously adapted to serve both purposes at once; and others having more special organs of aeration in the plumose tufts attached to the legs, jaws, and tail, as in *Cyclops* (Fig. 60).—There are certain Crustacea, indeed, which seem referrible as regards their general configuration to a higher type, but in which there is so little specialization of parts, that no distinct provision for respiration can be made out; and in these, moreover, the sanguiferous system is reduced to its zero of development, there being no dorsal vessel, and the flux and reflux of chylaqueous fluid in the general cavity being the only provision for conveying nutriment through the body (Fig. 105). This condition is in striking contrast with the centralized heart, minutely-ramifying vascular system, and elaborately constructed branchial apparatus, of the Crab; but even the latter retains a striking feature of imperfection in its organs of circulation, the sanguiferous current having still to pass through the general cavity of the body and the interstitial lacunæ of the limbs, in its transit from the ultimate ramifications of the arteries to the gills or to the heart.

Fig. 59.



Inferior surface of *Limulus*:—*a*, first pair of legs, used as prehensile organs; *b*, basal joints of five posterior pairs of legs, used as jaws; *c*, abdominal appendages bearing branchiæ; *d*, ensiform appendage.

Fig. 60.



A, female of *Cyclops quadricornis*:—*a*, body; *b*, tail; *c*, antenna; *d*, antennule; *e*, feet; *f*, plumose setæ of tail:—B, tail, with external egg-sacs:—C, D, E, F, G, successive stages of development of young.

54. In the class of *Arachnida* (Spiders, Scorpions, &c.), we find the

higher Articulated type presenting itself under another set of special modifications. These animals are adapted to breathe air like Insects, but by means of an apparatus of a very different kind; and they are destined to pass their lives under very different conditions. Instead of possessing wings and spending a large part of their time in active movement, they lurk for the most part in holes and hiding-places, and obtain their food (which is generally derived from living animals) by stratagem. The head and thorax are fused (as it were) into one mass, the cephalo-thorax; and to this all the members are attached. The tactile appendages possessed by Insects and Crustacea do not here present themselves; for the antennæ are wholly wanting, and the maxillary palpi are developed either into instruments of prehension, or into members resembling the thoracic limbs. Of true legs there are always four pairs; and this constitutes the most constant external character of the group. The tegumentary skeleton varies considerably as to its degree of firmness, in the different members of the class; in the Spider tribe, which may be regarded as its typical group, it is so soft throughout the abdominal region, that all appearance of segmentation is wanting; and although somewhat firmer in the cephalo-thorax, it does not serve, like the dense external skeleton of Insects and Crustacea, to give an unyielding support to the locomotive apparatus. It is interesting thus to observe the partial disappearance of one of the most characteristic features of Articulate structure, in a group which must be regarded as standing near the borders of its sub-kingdom. Another interesting modification is presented by the structure of the eyes: which, although more numerous than in Vertebrata (Spiders and Scorpions having six, eight, or even more), are formed upon the plan of the visual organs in that sub-kingdom. In the structure of the respiratory organs of the higher Arachnida, again, we find a decided approximation to the Vertebrated type, although they are still multiple, and open by special orifices in the segments in which they are situated, as in Insects.—Like the class of Crustacea, this group includes a large assemblage of forms, which, while they correspond in general *plan* of organisation, differ widely in *grade* of development. Thus, in the *Acarida*, it seems doubtful whether there is any proper circulating system; in the parasitic species generally, no special respiratory apparatus can be discovered; and in the lowest forms of this tribe, the sexes appear to be united, the ova being dispersed through the tissues of the body, instead of being developed within a definite ovarium. It is remarkable that, throughout this class, the young come forth from the egg in their complete form, or nearly so; and that even in the earlier stages of their development, the Arachnidan type is very distinctly differentiated from that of other Articulata, so that the embryo cannot be likened to any of the lower forms of that series.

55. We now arrive at the sub-kingdom VERTEBRATA, which unquestionably ranks as the highest division of the Animal Kingdom, since it contains those classes which display the greatest perfection of organised structure, as manifested in the special adaptation of each part of their organism to some different purpose, and in the consequent number and variety of their faculties. Whilst the apparatus of Nutritive life predominates in the Mollusca (the sensori-motor organs being only enough de-

veloped to enable the animal to seek its food, or to meet with an individual of the opposite sex, where the union of two is required for the purpose of generation), and whilst the activity of the Sensori-motor apparatus is the special characteristic of the Articulata, (whose actions seem to be almost entirely *instinctive*, that is, to be performed without any discernment or choice on their own parts), the Vertebrata are distinguished by the high evolution of that portion of the Nervous System,—the cerebrum and its dependencies,—which seems to minister to the operations of *intelligence*, wherein *means* are adapted to *ends* by the purpose and design of the individual itself. This attribute reaches its highest development in Man, whose entire organization is brought into subservience to it; but throughout almost the entire Vertebrate series, we see a decided tendency towards it; indications of reasoning power, and of the faculty of profiting by experience, being discernible even in the lower members of it. The predominance of the Nervous System is manifested, not only in the increased size of its centres, but also in the special provision which we here find, for the protection of these from injury. In the Invertebrated classes, with scarcely any exceptions, wherever the nervous system is enclosed in any protective envelope, that envelope serves equally for the protection of the whole body; this is the case, for example, in regard to the spiny integument of the Star-fish, the shell of the Mollusca, and the firm jointed rings of the Insect. Where exceptions do present themselves, they are in tribes which are near the higher borders of their respective sub-kingdoms, so as to abut (as it were) on the Vertebrate region; thus in the highest Crustacea, there is a set of internal projections from the shell, on each side of the median line, which form a series of arches partly enclosing the ventral cord; and in the naked Cephalopoda, the nervous centres are supported, and in part protected, by cartilaginous plates, which are evidently the rudiments of a true internal skeleton. It is by the high development and peculiar arrangement of the *Neuro-Skeleton*,—which not only encloses the nervous centres, but affords protection to the most important viscera, furnishes the system of levers required for the apparatus of locomotion, and affords fixed points for the attachment of the muscles whereby these levers are put in action,—that this sub-kingdom is most readily characterized. This neuro-skeleton, under all its special modifications, consists of a longitudinal series of *vertebræ;* each vertebra being composed of a *centrum*, a *neural arch* enclosing the nervous centres, a *hæmal arch* enclosing the centres of the circulation, and *lateral processes;* to which are frequently added *diverging appendages.* The several vertebræ may be very unequally developed, both as to size and differentiation of parts; thus we usually find those of the cranium (which never exceed four in number) much larger, and their components more elaborated, than are those of the caudal region, whose number is much less restricted. So, again, one or more of these components may be suppressed, the centrum being the element most uniformly present: or, on the other hand, any one or more of them may be extraordinarily developed. Thus in the cranium, especially of those higher Vertebrata whose cerebrum is large, the neural arches (Fig. 61, $^{1-15}$) are enormously expanded for its reception; whilst the hæmal arches of the three anterior of these vertebræ ($^{20-44}$) forming the bones of the face, are also considerably extended, and their elements remarkably modified in form. In the trunk, on the other hand, the neural arches are reduced to the dimensions of the spinal cord; whilst the hæmal are expanded, chiefly by the elongation of the lateral processes which are incorporated with them, so as to surround and protect the visceral mass. In front of this cavity, we find the hæmal portion of the occipital vertebra developed into the scapular arch (^{50}—^{52}); whilst behind it, the pelvic arch (^{62}—^{63}) is formed by a like development of the hæmal portion of one of the sacral vertebræ; and it is in the enormous development of the diverging appendages (^{53}—^{65}) of these vertebræ, that the anterior and posterior members originate. In the caudal region, the peripheral portions of the vertebræ are gradually suppressed; until at last nothing remains but the centrum.*

Fig. 61.

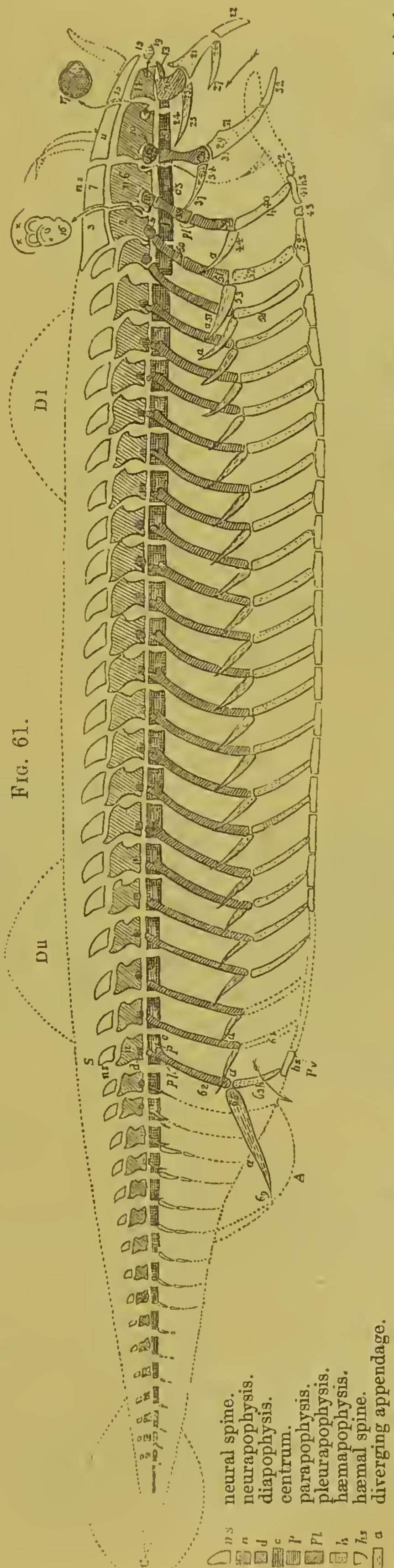


Diagram of *Archetype Vertebral Skeleton*, according to Prof. Owen, composed of the following parts:—1, basioccipital, 2, exoccipital, 3, supraoccipital, 4, paroccipital, constituting the neural arch of the first or Occipital vertebra of the head;—5, basisphenoid, 6, alisphenoid, 7, parietal, 8, mastoid, constituting the neural arch of the second or Parietal vertebra;—9, presphenoid, 10, orbitosphenoid, 11, frontal, 12, postfrontal, constituting the neural arch of the third or Frontal vertebra;—13, vomer, 14, prefrontals, 15, nasal, constituting the neural arch of the fourth or Nasal vertebra;—16, petrosal, or acoustic sense-capsule; 17, sclerotic, or ophthalmic sense-capsule; 18, 19, ethmo-turbinal, or olfactive sense-capsule;—20, palatine, 21, maxillary, 22, premaxillary, 23, 24, 25, pteregoid, 26, malar, 27, squamous, constituting the hæmal arch of the Nasal vertebra with its diverging appendages;—28, tympanic, 29-32, mandibular or lower jaw, 34-37, operculars, constituting the hæmal arch of the Frontal vertebra, with its diverging appendages;—38, stylohyal, 39, epihyal, 40, ceratohyal, 41, basihyal, 42, glossohyal, 43, urohyal, 44, branchiostegal, constituting the hæmal arch of the Parietal vertebra, with its diverging appendages;—50, suprascapula, 51, scapula, 52, coracoid, 52′, episternum, 53, anterior member, constituting the hæmal arch of the Occipital vertebra, with its diverging appendages; 58, clavicle, the hæmapophysis of the Post-occipital vertebra;—62, ilium, 63, ischium, 65-69, posterior extremity, constituting the hæmal arch of the Sacral vertebra S, with its diverging appendages; 64, pubis, the hæmapophysis of one of the lumbar (?) vertebræ. The chief osseous developments of the dermo-skeleton are added in outline, as the median horn supported by the nasal spine, 15, in the Rhinoceros; the pair of lateral horns developed from the frontal spine, 11, in most Ruminants; the median dorsal fins, D I, D II, in Fishes and Cetaceans; the caudal fin, C, and the anal fin A, in Fishes.

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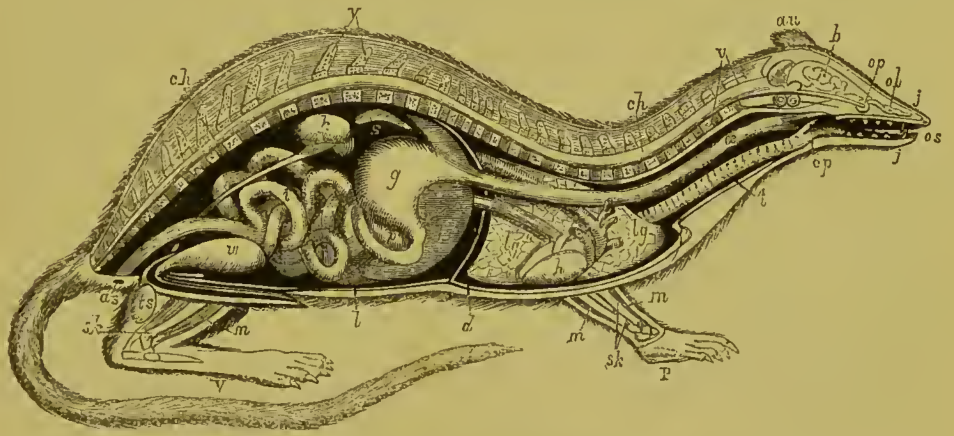
* The views of Professor Owen, as set forth in his masterly works on the "Homologies of the Vertebrated Skeleton," and on the "Nature of Limbs," as also in his "Lectures on Comparative Anatomy," vol. ii., are here followed.

56. The Vertebral skeleton, as a whole, is very differently developed in various parts of the series. Thus in the 'apodal' Fishes, locomotion is performed by flexion of the body itself; and here, as in the Worm tribe, we find the skeleton extremely flexible, and its divisions indistinct, the spinal column being a continuous cylinder of cartilage with scarcely a trace of segmentation. In the Serpent tribe, again, which is destitute of locomotive appendages, the vertebræ are extraordinarily multiplied, and are so connected by ball-and-socket joints, that the entire column possesses a most extraordinary degree of flexibility. In proportion, however, as distinct members are developed, and the power of locomotion is committed to them, we find the firmness of the spinal column increasing, and its flexibility diminishing: and in Birds—in which, as in Insects, the movements of the body through the air are effected by muscles that must have very firm points of support—the vertebral column is much consolidated by the union of its different parts, so as to form a compact framework. As a general rule, then, the mobility of the extremities, and the firmness of the vertebral column, vary in a converse proportion. The number of these extremities in Vertebrata, never exceeds *four;* and two of them are not unfrequently absent. The power of locomotion is not developed to nearly the same proportional extent as in the Articulata; the swiftest Bird, for example, not passing through nearly so many times its own length in the same period, as a large proportion of the Insect tribes: but it is far greater than that which is characteristic of the Mollusca; and there is no species that is fixed to one spot, without the power of changing its place. On the other hand, the highest Mollusca approach them very nearly in the development of organs of special sense, of which Vertebrata almost invariably possess all four kinds—sight, hearing, smell, and taste.

57. A like union of the characters of the Articulated and Molluscous sub-kingdoms, may be noticed in the general relations which the organs of Nutritive and those of Animal life bear to one another. The former, contained in the cavities of the trunk, are highly developed; but, as in the Mollusca, they are for the most part unsymmetrically disposed. Of the latter, the nervous system and organs of the senses occupy the head, whilst the muscles of locomotion are principally connected with the extremities; both are symmetrical, as in the Articulata; but, whilst that part of the nervous centres, which is the instrument of reason, is very largely developed, the portion which is specially destined to locomotion, together with the muscular system itself, bears much the same proportion to the whole bulk of the body, as it does in the Articulated series. Hence we observe that the Vertebrata unite the unsymmetrical apparatus of nutrition, characteristic of the Mollusca, with the symmetrical system of nerves and muscles of locomotion, which is the prominent characteristic of the Articulata; both, however, being rendered subordinate to the great purpose to be attained in their fabric—the development of an organization through which *intelligence* may peculiarly manifest itself. For the operation of this, a degree of *general* perfection is required, which is not manifested elsewhere; and, in order that the body may be always in a state of readiness for active exertion, it is requisite, not merely that it should be adequately nourished, but that it should be constantly maintained at a high temperature. This is fully the case, however, with only the two higher classes of Vertebrata; which, in their power of gene-

rating sufficient heat to counteract the effect of external vicissitudes, and in the uniformity of their rate of vital activity, contrast strikingly with the Invertebrated classes. Indications of a like power, however, though less energetic in its operation, are presented in Reptiles and Fishes. The maintenance of a constantly-high temperature, and the support of the system under the demands created by its unceasing activity, involve an energetic performance of the functions of respiration and circulation; and these again require a constant supply of alimentary material, and great activity in the process of digestion. The Digestive apparatus usually presents a high degree of specialization; its simplest forms (as among the Invertebrata) being found in those tribes which obtain their food by the suction of animal juices, and its most complicated in the vegetable-feeders. Not only do we almost invariably find the stomach anatomically separated by valvular constrictions from the œsophagus and intestinal tube, but it is completely differentiated from them in function also; the intestine itself generally exhibits varieties of conformation and of endowments in different parts of its course; and the number and complexity of its accessory glands is greatly augmented. The anterior part (considering the animal as placed horizontally) of the visceral cavity is usually occupied by the heart and respiratory organs, and the posterior by the digestive and excretory apparatus; it is only in Mammals, however, that the separation between these portions is completely made, by the interposition of a diaphragm. The general cavity of the body is now altogether cut-off from participation in the transmission of nutritive fluid; a special system of vessels being interposed for the absorption of sanguifying materials, alike from the digestive cavity, and from the interstitial lacunæ of the tissues generally, and for the introduction of these into the blood-current; whilst the proper sanguiferous system of vessels forms a completely-closed circuit. All Vertebrata (save the *Amphioxus*) have red blood, which is

Fig. 62.



Ideal Section of a *Mammal*, illustrating the Vertebrate type of structure:—P, pectoral extremities; V, ventral extremities; *as*, anus; *au*, organ of hearing; *b*, brain; *ch*, *ch*, spinal chord; *d*, diaphragm; *ep*, epiglottis; *g*, stomach; *h*, heart; *i*, intestine; *j*, *j*, jaws; *k*, kidney; *l*, liver; *lg*, lung; *m*, *m*, muscles; *œ*, œsophagus; *ol*, organ of smell; *op*, organ of vision; *os*, mouth, containing organ of taste; *p*, pancreas; *s*, spleen; *sk*, *sk*, skeleton; *t*, trachea; *ts*, testis; *u*, urinary bladder; *v*, *v*, vertebral column.

put in motion by a single distinct muscular organ, the Heart; and the Respiratory organs, whether formed for aquatic or for atmospheric respiration, are always placed in immediate connection with that organ, so as to receive a stream of blood directly from it. The respiratory apparatus, moreover, always draws-in its supplies of the aerating medium, whether air or water, through the mouth; and these supplies are renewed by means of rhythmical muscular movements, sustained by an automatic action of the nervous system. The rest of the apparatus for the depuration of the blood presents a very high development in the Vertebrated classes; the structure of the glands by which it is effected being such, as to combine the greatest functional activity with the closest concentration of the organic mechanism concerned in it.

58. The power of Reproduction by gemmation is limited in this series to the reparation of lost or injured parts, and nowhere extends (save at an early period of the evolution of the germ, when its grade of development corresponds with that of the simpler Zoophytes*) to the multiplication of independent 'zooids.' The two kinds of generative organs being never combined in the same individual, the concurrence of two of opposite sexes is required for each generative act. In the lower Vertebrata, it is sufficient that the products of the male and female organs should come into contact after their extrusion from the body; but in the higher, the ova are fertilized while yet within the body of the female, and are commonly retained there for a shorter or longer time afterwards. In nearly all Vertebrata, the young animal, when it first comes forth into the world, has the characters of the class to which it belongs; and those of its order, family, genus, and species, if not at once distinguishable, speedily become so, the special type being evolved out of one more general, without any true metamorphosis: such a metamorphosis, however, does take place in one remarkable group, that of *Amphibia* or Batrachian Reptiles; the members of which come forth from the egg in the form and condition of Fishes, and gradually assume that of Reptiles by a series of changes in which every part of their organism is concerned.

59. The Vertebrate type of structure displays itself under four principal aspects; in comparing which we can scarcely fail to recognise the difference so frequently insisted-on, between *grade* and *plan* of development. For the Physiologist has no hesitation in affirming, that, whilst each of the classes of Fishes, Reptiles, Birds, and Mammals, has a certain characteristic conformation that is typical of it, they may be regarded as parts of a series, which on the whole ascends with considerable regularity from the lowest Fish to the highest Mammal; since he traces in every one of the chief divisions of the organism, alike in the apparatus of animal and in that of vegetative life, a gradual progress from a simpler and more general to a more elaborate and specialized type. This is peculiarly obvious in the organs of Circulation and Respiration, and in those of Reproduction; and it is from these, accordingly, that the Naturalist draws his best characters for the separation of the four classes in question. Thus in Fishes, which are specially adapted for an aquatic life, the

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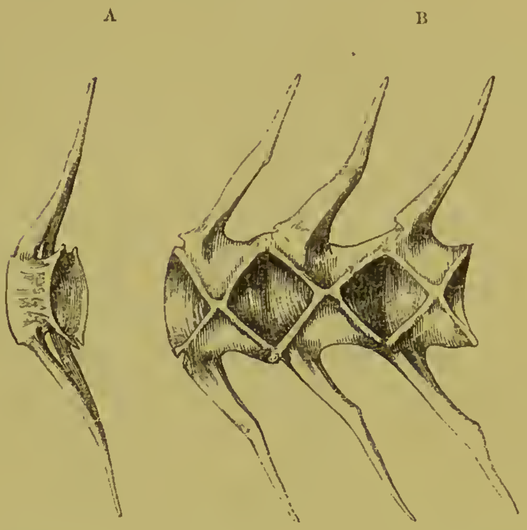
* The admission of this exception will be hereafter shown (CHAP. XI.) to be required by the present state of our knowledge in regard to the formation of *double monsters*.

aeration of the blood is accomplished by gills, as in the Mollusca, and the heart (as in that sub-kingdom) possesses only a single auricle and ventricle; but the relation of the heart to the branchial circulation, and the mechanical arrangements for renewing the water in contact with the gills, are such as to afford to the blood of this class a far higher degree of oxygenation, than that which the circulating fluid of the Mollusks can receive. The three higher classes of Vertebrata are organized for atmospheric respiration; but to this, in Reptiles, only a part of the blood is subjected; the heart usually possessing only three cavities, and the blood transmitted to the system being a mixture of that which has been just returned from it in a venous condition, with blood that has been arterialized by transmission through the lungs. On the other hand, in Birds and Mammals, the arrangement of the circulating apparatus is such, that the pulmonary and systemic circulations are completely separated, each having its own heart, and the one following upon the other; so that the whole current of blood is alternately transmitted to the system and to the lungs, and what has returned from the tissues in a venous state is entirely oxygenated before being transmitted to them a second time. But these two classes, whilst separated from Fishes and Reptiles by the type of circulating and respirating apparatus which they both present, are separated from each other by the mode in which their generative function is performed; Birds, like Fishes and Reptiles, being oviparous; whilst Mammals retain their ova within their bodies, until the embryo is sufficiently advanced in its development for it to be nourished externally by mammary suction.—As the structure and action of the principal organs of Vertebrata will hereafter be considered in detail, it will be sufficient here to indicate the general plan of conformation which prevails in each class respectively, and especially that part of it which is exhibited in the structure of the skeleton.

60. The skeleton of *Fishes* departs less from the 'archetype,' than does that of either of the other classes; but it presents, nevertheless, certain special modifications, that adapt it to the peculiar conditions under which these animals are destined to exist. Thus with a low development of the neural arches of the cranial vertebræ, in conformity with the small size of the brain, we find the hæmal arches of great size; the greater part of their expansion being destined to give to the buccal apparatus the power of prehension, which is necessitated by the absence of prehensile power in the limbs; whilst certain of their elements are specially adapted to afford support and protection to the respiratory apparatus. So in the conformation of the skeleton of the trunk, we find its lowness of type indicated by the 'vegetative repetition' of similar parts; the vertebral segments differing much less from each other, than they do in any of the higher animals save Serpents, so that no distinction into regions is marked-out. The vertebræ, too, are very loosely framed together, so that great freedom of motion is permitted in a lateral direction; the support everywhere given by the medium which these animals inhabit, preventing the necessity that exists in higher animals for such a close connection of different parts of the framework, as shall enable it to rest securely on a limited number of points. The most remarkable peculiarity which this condition involves, is the cupped form

of each of the surfaces of the 'centra' or bodies of the vertebræ (Fig. 63), which work over an intervening series of doubly-convex intervertebral capsules, in such a manner as to impart great freedom of movement to the entire column. It is by lateral strokes of the tail and posterior part of the trunk, whose surface is extended by the vertical median fins, that the acts of locomotion are chiefly effected; the functions of the pectoral and ventral fins, which answer to the anterior and posterior members of higher animals, being generally limited to balancing the body and changing its direction. There are certain cases, however, in which the enormous development of the pectoral fins enables them to serve as the special instruments of locomotion; and when this is the case, the spinal column is shorter and less flexible than usual. The 'rays' upon which the median fins (dorsal, caudal, and anal) are supported, belong, not to the vertebral but to the dermal skeleton; as do also, it seems probable, the intercalary bones that support them, which are implanted between the neural spines of the vertebræ. In the pectoral fins, which are always situated immediately behind the head, in connection with the occipital segment from whose hæmal arch they are developed, the arm and fore-arm do not manifest themselves externally, being hidden within the trunk; the extended surface of these fins is consequently given by the elongation and multiplication of the carpal, metacarpal, and phalangeal bones; and their movements are limited to flexion and extension at the wrist-joint. There is no sternum in Fishes, the hæmal arches of the dorsal vertebræ being never closed-in beneath; and the scapular arch is consequently destitute of the support which it elsewhere derives from that bone, being only completed by the meeting of the coracoids on the median line. The ventral fins, which are formed upon the same general plan with the pectoral, have no fixed position: for the pelvic arch is not connected with the spinal column in any other way than by a ligamentous band, and there is no such consolidation of two or more vertebral centra for its support, as elsewhere constitutes a 'sacrum.' In those fishes especially, which enjoy a considerable range of depth, the ventral fins are advanced towards the head, being sometimes situated even in front of the pectorals.—The dermal skeleton of Fishes is usually more developed than it is in the higher classes, and comes into closer connection with the neuro-skeleton. It sometimes forms a complete bony envelope to the entire body, and seems to have done so especially in the Fishes of the earlier periods of the world's history; but the general investment more

Fig. 63.



A, Oblique view of the *Vertebra of a Cod;* B, Section of three connected vertebræ, showing the intervertebral spaces.

commonly consists, in the existing Fishes, of thin plates, whose structure is essentially cartilaginous, though true osseous tissue is still commonly found in the dermal 'rays' and intercalary bones which support the median fins. To the dermal skeleton, moreover, may be referred the Teeth; which in this class approximate much more closely in structure to bone, than they do in Reptiles or Mammals; and become more intimately connected with the bones of the jaw, so as to be even joined-on to them by continuous ossification.

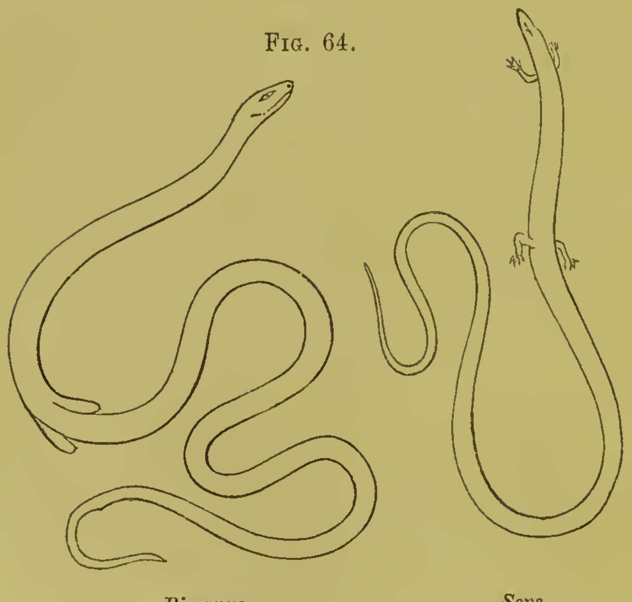
61. In the Muscular and the Nervous apparatus, we observe the same tendency to vegetative repetition of similar parts, coupled with special developments for particular purposes, as we have noticed in the skeleton; and the cephalic centres of the latter are remarkable for the very small size of the Cerebrum, in proportion to that of the sensorial centres. The Sympathetic system of nerves, moreover, is not distinctly differentiated in some of the lower Fishes from the cerebro-spinal; and even in the higher, it retains a peculiarly intimate connection with the pneumogastric nerve. The generative apparatus of Fishes generally, although in some respects higher in type than that of the Invertebrata, is lower in grade of development; there is no intromittent organ, the ova being fertilized, after they have been deposited, by the casual contact of water through which the male semen has been diffused. The embryo at the time of its emersion from the egg, is far from having acquired all its parts and organs, and depends for some time upon the store of food contained in the yolk-bag which hangs down from the abdomen; and the young receives no care or sustenance from its parents. In the higher Cartilaginous fishes, on the other hand, there is a true sexual congress, so that the ova are fertilized within the body; and they are sometimes delayed there until an advanced period of the evolution of the embryo, deriving additional supplies of nutriment from the parent during the latter part of this period. And it is worthy of special remark, that with this prolongation of the period during which the embryo is supported from external sources, a much higher grade of development is ultimately attained by many organs, especially by the nervous system.

62. The class of *Reptiles* includes a collection of animals of very diversified conformation, which nevertheless agree in certain leading peculiarities of anatomical structure and physiological action, that distinguish them from all other Vertebrata. They are for the most part adapted to inhabit the surface of the earth, along which they creep or crawl, rather than run or leap; and those which live in water are obliged (with few exceptions) to come to the surface to breathe. The arrangement of their circulating and respiratory apparatus, however, being such as to aerate only a part of the blood-current, their demand for oxygen is far less energetic than that which exists in other Vertebrata: and they can endure a longer privation of it. This want of respiratory activity is (so to speak) the manifestation of that general inertness, both of the organic and of the animal functions, which is the distinguishing physiological character of the class. Their demand for food is not frequently repeated, and they can sustain a very long privation of it; their perceptions are obtuse, and their movements are sluggish; altogether they may be said to live very slowly, though their degree of vital activity varies with the temperature. There is a marked general accordance, again, among all the orders of

Reptiles, in the degree of development of the cerebrum, as compared with the sensorial centres; this being intermediate between the almost rudimentary condition under which that organ usually presents itself in Fishes, and the greatly-augmented size which it possesses in Birds.

63. The differences between Frogs, Serpents, Lizards, and Turtles, are most apparent in the skeleton; but these depend rather upon the suppression of certain parts, and upon the excessive development of others, than upon any essential diversity of type. The skeleton of a Lizard, at the first view, does not present any marked difference from that of a Mammal. We find an evident distinction between neck, trunk, and tail; and both the anterior and posterior extremities now have a fixed position, and are so connected with the spinal column that the weight of the body may be supported on them. In no existing Reptiles, however, are more than two vertebræ united to form a sacrum; so that the junction of the pelvic arch with the spinal column cannot possess the same firmness as in Mammals, whose sacrum is usually composed of from four to six segments. The total number of vertebræ is often very considerable, but the multiplication is chiefly in the *caudal* region; and the caudal vertebræ are remarkable for having their hæmal arches continued backwards like the neural, forming what are known as the chevron-bones. The most distinctive peculiarity in the skeleton of the trunk, is the backward prolongation of the sternum and of the sternal ribs over a considerable part of the abdominal region. The bones of the extremities are externally formed nearly upon the plan of those of terrestrial Mammals; but differ from them in the inferior degree of development of processes for muscular attachment, and in having no medullary cavity, their interior being occupied throughout by cancellated structure. Their dimensions are proportional to the weight which they have to sustain, and to the use that is to be made of them in the act of progression; and we may pass from the order of Lizards towards that of Serpents through a continuous series of forms (Fig. 64), in which the limbs become more and more feeble until we lose all external traces of them, whilst at the same time the body becomes more elongated and serpent-like. In the true Serpents, the locomotive power is entirely withdrawn from the limbs (the rudiments of which, where they exist, are applied to the purpose of 'claspers' in copulation); and not only are the scapular and pelvic arches rudimentary, but the sternum is

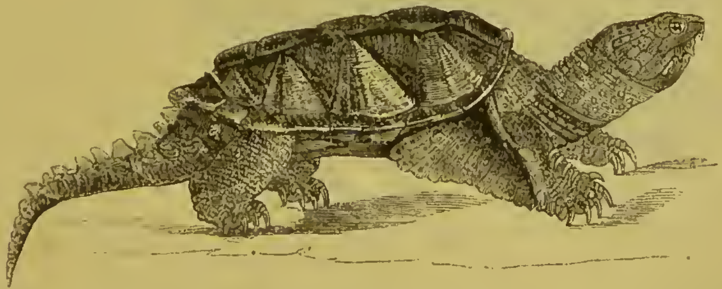
Fig. 64.



Bimanus. *Seps.*

entirely undeveloped, so that the extremities of the ribs are free, as far at least as the endo-skeleton is concerned. On the other hand, the body is immensely elongated, chiefly by the multiplication of the *dorsal* vertebræ; thus in the *Python*, the total number of vertebræ is 422, of which about six-sevenths possess ribs. The spine is extremely flexible; and the ribs, whose extremities are connected with the abdominal scuta of the integument, can be employed in some degree as instruments of progression, moving backwards and forwards beneath the skin. In the elongated and cylindrical form of their bodies, in the multiplication of its segments, and in their mode of progression, Serpents bear a striking analogy to the Iulidæ (Fig. 54). Their internal organization partakes of the general elongation; for one of the lungs (the other being very little developed) and the ovary extend, like the intestinal tube, through a large part of the cavity of the trunk; and the liver and kidneys are also considerably lengthened, although not to the same degree. In the structure of the nervo-muscular apparatus, there is a remarkable degree of 'vegetative repetition,' as in the lower Articulata; for the spinal cord, although forming a continuous column, is of nearly the same diameter throughout, resembling in this respect the gangliated ventral cord of the Myriapods; and the successive pairs of intervertebral nerves which it gives off, supply muscles whose form and arrangement are almost exactly the same, from one end of the body to the other.—In the *Batrachian* Reptiles (Frogs, &c.), a modification of precisely the opposite character is superinduced upon the ordinary Reptilian conformation; for the body is shortened, not merely by the non-development of the tail (at least in the *Anoura*, which are the types of the group), but also by a reduction of the number of vertebræ of the trunk; whilst, on the other hand, the extremities are enormously developed, locomotion being entirely performed by their agency; the ribs, moreover, are undeveloped, but the sternum is of large size, so as to give protection to the viscera, as well as attachment to the muscles which cover them.—Another still more remarkable modification is presented in the *Chelonia* (Turtles, &c.), which have the body enclosed within a 'shell' formed of a *carapace* and *plastron;* the carapace or dorsal arch being formed by the coalescence of dermal bones with the expanded ribs; whilst the plastron

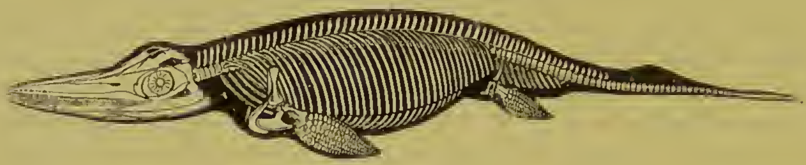
FIG. 65.



Emysaura Serpentina.

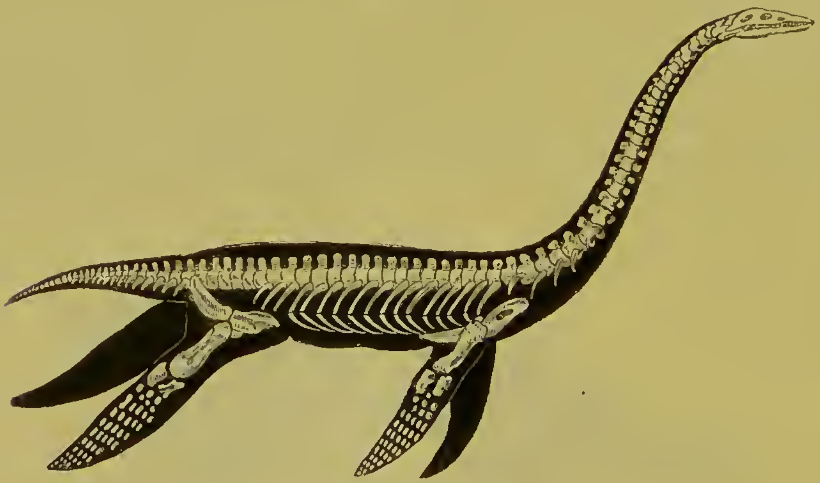
or ventral shield, is formed by an expansion of the sternum and sternal ribs, still further extended by the development of portions of the dermal skeleton in continuity with them. The spinal column is here completely immovable, the vertebræ being anchylosed to each other and to the carapace; so that the act of locomotion is completely delegated to the extremities, the bones of which are highly developed. A transition between the Chelonia and the Sauria is established by such animals as the *Emysaura* (Fig. 65); which have the shell so contracted, and the neck, tail, and limbs, so much elongated, that these cannot be drawn within it; and which have at least as much of the Alligator as of the Tortoise in their general habits.—Besides the existing orders of Reptiles, we are acquainted with fossil remains, which must be referred to this class, but for the reception of which three additional orders must be formed; and it is interesting to remark that these orders may be considered as *representing* the other three classes of Vertebrata. Thus, the *Enaliosauria*, of which the Ichthyosaurus (Fig. 66) and the Plesiosaurus (Fig. 67) are the types, are Lizard-like animals adapted to lead the life of Fishes; their vertebræ being biconcave as in that class, and the whole skeleton of the trunk having an extraordinary mobility; but the act of locomotion having been chiefly performed by the members, which are constructed rather upon the plan of the paddles of the Cetacea (though with a 'vegetative repetition' in the number of phalangeal

Fig. 66.



Skeleton of *Ichthyosaurus*.

Fig. 67.



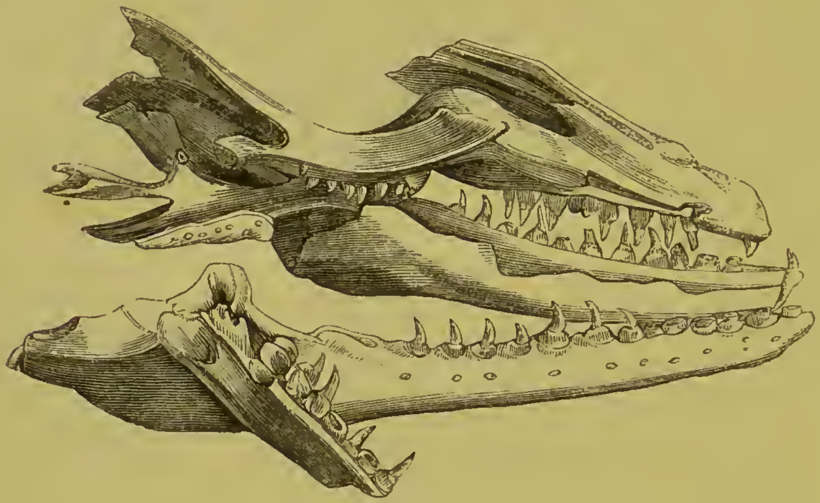
Skeleton of *Plesiosaurus*.

bones), and are connected with the spine by scapular and pelvic arches of remarkable strength.—So, again, in the *Pterodactylus* we find the ordinary Saurian type adapted to a Bird-like life: the chief modification being in the anterior extremities, which have a single digit enormously lengthened for the support of a wing-like expansion (Fig. 1); but various peculiarities, bearing upon the same end, being observable in other parts of the skeleton, which were doubtless connected with analogous modifications of its internal organization. Of these, the hollowness of the wing-bones, which so strongly resemble those of certain longipennate Birds as even to have been mistaken for them, is one that is interesting from its physiological relations.—Lastly, the Mammalia seem to have been represented in the order *Dinosauria*, consisting of gigantic Reptiles which were elevated upon much longer limbs than existing Lizards; for their skeletons present several features of analogy to that class, the snrfaces of the vertebræ being generally flattened, the ribs being connected with the vertebræ by a double articulation, at least five vertebræ being consolidated into a sacrum, so as to give a very firm basis to the pelvic arch, and the bones having a central medullary cavity.—Notwithstanding these and other modifications of the Reptilian type, its essential characters are obviously maintained in all the foregoing orders; and these are peculiarly manifested in the structure of the cranium.

64. The vertebral elements of the Reptilian cranium, although not as distinct from each other as in the Fish, undergo far less coalescence than in warm-blooded animals; and the number of bones which remain separate, is therefore very considerable. Thus in the Crocodile, although one of the highest existing forms of the class, the four pieces of the neural arch of the occipital segment, which coalesce to form the 'occipital bone' of Man, remain permanently distinct; so, again, the 'sphenoid bone' is represented by six pieces, the 'frontal bone' by three, and the 'temporal' by four. In all the scaly Reptiles, the occipital segment is articulated with the vertebral column by a single condyle formed by its centrum, which is received into a hollow in the body of the 'atlas' (or first vertebra of the neck), just as the convexity at the back of each ordinary vertebra is received into a concavity of the vertebra behind it: in the naked-skinned Batrachia, however, the connection is made by a double condyle,—a character which alone serves to distinguish the skull of any of these animals, from that of all other Reptiles. In the Perennibranchiate forms of this order, the general conformation of the skull, as well as of other parts of the skeleton, presents a very close approximation to the ichthyic type. The skull of Serpents is chiefly remarkable for the extraordinary dilatability of the entrance to the mouth; which is especially due to the want of union between the two halves of the lower jaw on the median line, and to the mobility of the elements of the tympano-mandibular arch with which it is articulated; but partly also to the imperfect approximation between the bones of the upper jaw, which have only a ligamentous connection with each other. In the Chelonia, on the other hand, the component pieces of the jaws are very firmly united to each other; and an increased extent is given in the Marine Turtles to the surface of attachment for the powerful temporal muscle, by the addition of a bony arch covering its exterior,—this, however, not being an entirely

new structure, but being formed by expansions proceeding from the parietal, posterior frontal, malar, squamosal, and mastoid bones. With the exception of the Chelonia, nearly all Reptiles possess a dental apparatus, which is intermediate in its structure and mode of development between that of Fishes and that of Mammals. For, save among a few extinct genera, all Reptiles possessing teeth exhibit more or less of approximation to the formation of sockets for their reception; and a very interesting correspondence may be traced between the various grades of such approximation, and the successive stages of dental development in the embryo of higher animals. Thus whilst, in the extinct *Mososaurus*, the tooth is simply anchylosed at its base to the margin of the jaw (Fig. 68),—no dental groove having ever been formed, but only dental papillæ,—in the greater number of ordinary *Lizards* and *Frogs*, the alveolar ridge is elevated on the outer margin of the jaw (the teeth being anchylosed to it), so as to form the outer wall of the dental groove, as in a Human embryo of about the 7th week; in the extinct *Ichthyosaurus*, this groove is completed by a corresponding elevation of the inner margin of the jaw, and an indication is presented of transverse division into sockets, as in a Human embryo somewhat more advanced; in most *Serpents* and some *Batrachia*, the teeth are surrounded by shallow sockets, to which their bases become adherent; whilst in the extinct *Plesiosaurus* and the whole *Crocodilian* group, the sockets are deep enough to give firm hold to the teeth, which remain free as in Mammals. The base of the teeth in Reptiles, however, is seldom contracted into a 'fang'; and in no instances are Reptilian teeth implanted like those of Mammals by diverging fangs. The form and structure of the teeth in this class are for the most part conformable to one simple plan, there being very little differentiation as to either; they seldom depart much from the simple cone, more or less acute at its point, and are obviously adapted more for seizing and holding prey, than for dividing and masti-

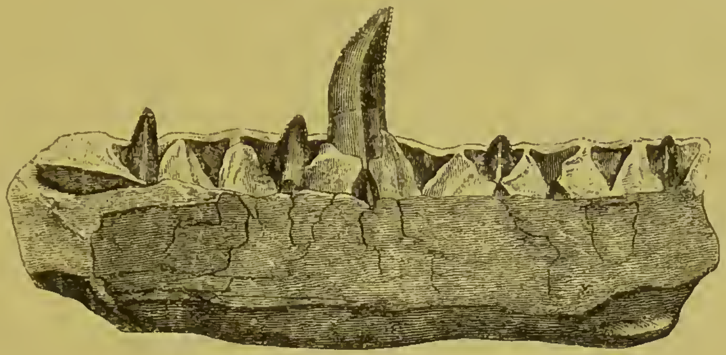
Fig. 68.



Skull of *Mososaurus*.

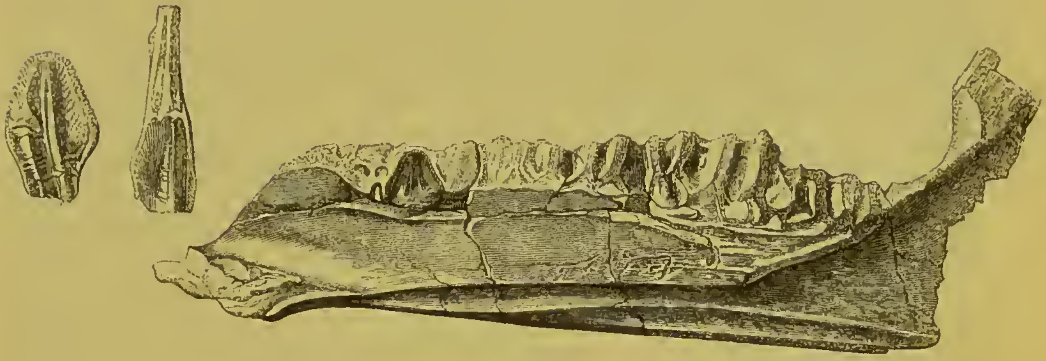
eating food; and their most remarkable modifications, one for carnivorous (Fig. 69), and the other for herbivorous regimen (Fig. 70), are seen

FIG. 69.



Portion of jaw of *Megalosaurus*.

FIG. 70.



Portion of lower jaw and teeth of *Iguanodon*.

in two genera of the extinct order of *Dinosauria*, which in many other particulars appear to have approached Mammalia. In the entire order of *Chelonia*, the teeth are replaced by a horny beak, which is developed, like the teeth, from a number of distinct papillæ along the margins of the jaw-bones; and the same is the case with the larvæ of the *Batrachia*, which, however, cast off the beak when they assume the perfect Reptilian condition, their jaws then becoming furnished with teeth.

65. The class of *Birds* may be considered as the *physiological antithesis* to that of Reptiles; its *plan* of development being far more completely opposed to that which prevails in the last-described class, than is that of Mammals; though as regards the *grade* of development of the greater number of their organs, Birds are manifestly intermediate between Reptiles and Mammals.—Taken as a whole, the members of this class exhibit a remarkable conformity to one general type, presenting in this respect a marked contrast to the diversity which we have seen to prevail amongst Reptiles; and this conformity is both structural and physiological, being shown alike in the plan of organization, and in the working of the organic mechanism. They have been denominated, and not inappropriately, "the Insects of the Vertebrated series;" possessing as they do a series of

adaptations for passing their lives, not upon the solid ground, nor in water, but in the elastic and yielding air, which are very analogous (though, from the difference between the Vertebrated and Articulated types, they cannot be homologous) to those which form the essential characteristics of Insects. This is especially obvious in the extension given to the respiratory apparatus through a large part of the fabric; which has the double effect of adding to the respiratory surface, in the degree necessary for that perfect oxygenation of the blood which is required to sustain their wonderful activity of movement, and of diminishing the specific gravity of the body by the substitution of air for more weighty matters. Birds, again, resemble Insects in the complete delegation of the locomotive power to the members, and in the consolidation of the skeleton of the trunk; and the movements of flight are performed in a manner essentially the same, although the wing of the Bird has no anatomical relation to that of the Insect, being rather the representative (so far as any part of a Vertebrated animal *can* represent a part of an Articulated) of its anterior legs.—Birds stand in remarkable contrast with Reptiles, moreover, in the energy with which all their vital operations are performed. The high degree of nervo-muscular activity which they put forth, can only be kept-up by a very energetic performance of the nutritive processes; and this involves, and is at the same time subservient to, the maintenance of a very elevated temperature (100°—112°). Some Insects, during the period of their greatest activity, generate as much heat as Birds; but they cannot sustain this, and are consequently liable (like cold-blooded animals generally) to be reduced to a state of complete torpidity by a depression of external temperature, which Birds have the power of resisting. In the tegumentary covering of Birds, we have a most remarkable combination of attributes; for it serves alike to retain the animal heat within the body, in virtue of its non-conducting power, and to give the required expansion of surface to the wings. It is only in a few birds which are incapable of flight, that we find any considerable modification of this important feature; the Penguin, which has many Reptilian affinities, having the feathers on the anterior members (which act as fins in propelling the bird through the water) metamorphosed into the likeness of scales; while in the several members of the Ostrich tribe, which usually have wings still more undeveloped than those of the Penguin, and which are only fitted for progression by running like Mammals upon their elongated legs, the feathers present closer and closer approximations to hairs.

66. The bony frame-work constituting the Bird's vertebral skeleton, presents a series of peculiarities which distinguish it most completely from that of other Vertebrata; and, as in Reptiles, there is no part more characteristic of the class, than the cranium. Whilst that of Reptiles is remarkable for a permanent separation of a great number of its vertebral elements, that of Birds is no less remarkable for the close union which very early takes place among these, so that the sutures between the different portions of the neural arches are abolished, and the whole brain-case seems formed of a single piece. The bones of the face, however, do not undergo the same consolidation; for they are always so connected with those of the cranium, as to possess considerable mobility; and their union among themselves is seldom complete. In the mode of

articulation of their lower jaw, Birds agree with other Oviparous Vertebrata, and differ from Mammals; for the tympanic portion of the temporal bone remains distinct from the rest, and forms, as in Reptiles and Fishes, a pedicle interposed between the jaw and the solid part of the cranium. Each ramus of the jaw is originally formed, as in Reptiles, of six pieces; but whilst these remain permanently distinct in Reptiles, their coalescence begins very early in Birds; and this goes on until the number of pieces is reduced to three on either side; whilst by the coalescence of the two which touch on the median line, the total number of pieces is further reduced to five. It is interesting to remark that the traces of the original separation of these elements remain longest in those aquatic Birds, which show in other parts of their conformation the closest approximation to the Reptilian type. The skull, as in most Reptiles, is still articulated with the vertebral column by a single tubercle, formed by the centrum of the occipital vertebra; an incipient separation of the articulating surface, however, into two lateral halves, being occasionally presented.—The length of the neck, and the number of vertebræ of which it is composed, vary considerably in the different tribes of birds, and seem in each to have reference to its own peculiar requirements; thus in the long-legged Waders and Struthious birds, the neck seems elongated for the purpose of enabling the head to reach the ground without flexure of the limbs; whilst in the Swan and other short-legged aquatic birds, we find a similar elongation, the purpose of which is obviously to allow the bill to be plunged deep into the water in search of food, whilst the body is floating on the surface. The tail, on the other hand, is always very short, or even almost rudimentary; and it serves no other purpose than to support the tail-feathers, by whose agency the birds of active flight are steered as by a rudder. Whilst the cervical vertebræ are connected with each other in such a manner as to ensure great mobility (synovial capsules being interposed between their articulating surfaces, in the place of intervertebral fibro-cartilage), those of the dorsal region (especially in Birds of active-flight) are so united, as to provide for the greatest fixity that is compatible with the degree of mobility required in the osseous framework for respiratory and other purposes. The ribs have for the most part a double articulation with the spinal column; and they are prevented from moving too freely upon each other, by the splint-like processes ('diverging appendages') which project from the posterior margin of each, and overlap the rib behind it, to which it is attached by fibrous ligaments. The spinal ribs are connected with the sternum by true osseous sternal ribs, which have regular articulations at each end, so as to allow freer motion to the sternum for the alteration of the capacity of the thorax. The sternum is more remarkably developed in Birds than in any other Vertebrata; being so augmented in length and breadth, as to cover the ventral surface of a great part of the abdominal as well as of the thoracic cavity; and usually having its central part elevated into a keel or ridge, the degree of prominence of which bears a regular proportion to the strength of the pectoral muscles, and consequently to the power of flight. The ribs being developed from all the vertebræ between the scapular and pelvic arches, the usual 'lumbar' region would seem to be wanting in Birds; but this is probably due to its absorption (so to speak) into the sacral region; for the iliac bones are prolonged very far forwards, and are connected with a far larger number of vertebræ than we elsewhere find giving support to them, the number of segments in the sacrum of Birds being scarcely ever less than 10, and being augmented, especially in Birds whose support and locomotion chiefly depend upon the posterior extremities, even to 19.—The scapular arch is still formed upon the plan which prevails through the lower Vertebrata; the principal connection of the scapula with the sternum being effected by means of the coracoid bone, whilst an independent clavicular arch, the degree of development of which varies greatly in different tribes of Birds, is formed by the union of the two clavicles on the median line, constituting the 'furcula.' The anterior extremity is chiefly remarkably for the longitudinal extension and lateral consolidation of the bones of the hand; only two carpals and two metacarpals being distinguishable (the latter anchylosed together), and only one digit attaining any considerable development (Fig. 2) though rudiments of a thumb and of one or two additional digits are usually traceable. The osseous framework of the wing is destined simply for the attachment of muscles, and for the support of the integument in which the wing-feathers are implanted; it being by these, and not by any continuous expansion of the skin itself (as in Bats and the extinct Pterodactyles) that the required surface is afforded. The pelvic arch is not merely remarkable for the great number of sacral vertebræ which are anchylosed to form its support, but also for the separation of its two lateral halves at the median symphysis; its incompleteness at that part appearing to have reference to the relatively-larger size of the eggs of Birds, whilst the extraordinary elongation as well as peculiar firmness of the sacro-iliac symphysis would seem intended to compensate for this deficiency. In the conformation of the lower extremity, we have chiefly to notice that the femur remains short, even when the general elongation of the limb is the greatest; it being in the tibia and metatarsus that the greatest variations occur. The fibula is rarely present as a separate bone, being usually anchylosed with the tibia, and being sometimes almost undistinguishable. The tarsal bones are anchylosed with the metatarsal at an early period in the life of most Birds; and the metatarsus appears to consist of but a single bone, although there are indications that it contains the elements of three, these remaining distinct in the Penguin for a considerable part of their length. The foot usually possesses four digits, with sometimes the rudiment of a fifth; but in some of the Struthious birds we find the number reduced to three, or even two. The number of phalanges is five in the fourth or outermost digit, but diminishes regularly to two in the first or innermost.

67. As might be expected from the analogy of Birds with Insects, and from the large proportion of their body that is occupied with the apparatus of locomotion, the organs of nutrition are comparatively small; but what is wanting in size is made up in functional activity. The remarkable development of the instinctive propensities is another interesting point of correspondence between the two classes; there being this difference, however, between them, that whereas the actions of Insects appear to be entirely governed by these propensities, those of Birds are modified by their intelligence. In respect to this attribute, as

in the development of the Cerebrum which is its instrument, Birds appear to be strictly intermediate between Reptiles and Mammals; and in the general structure of their sensorial apparatus a like position is indicated, whilst in particular points of conformation they differ from both these classes.—It is interesting to observe how, without any essential departure from the type of Generative apparatus which prevails among the lower Vertebrata, a much higher physiological character is here imparted to the function. The store of nutriment provided in the egg for the embryo, is very much larger in proportion to the bulk of the animal; so that its development can be carried-on to a higher point, before it is thrown upon its own resources. Again, the evolution of the germ, and its appropriation of the nutriment thus provided, are promoted by the high temperature which is constantly imparted by the body of the parent. And even after its emersion from the egg, the young Bird generally remains for some time more or less dependent upon its parent for warmth and nurture; this dependence being usually most prolonged and complete, in Birds whose faculties ultimately attain the highest elevation.

68. The *Mammalia* are universally admitted to form the highest group in the Animal Kingdom; not only as being that to which Man belongs, but also as possessing the most differentiated organization, adapted to perform the greatest number and variety of actions, and to execute these with the greatest intelligence. This high development is obviously connected with that greatly-prolonged connection between the parent and the offspring, which is the special characteristic of the class. The ovum of Mammals is very small in comparison with that of Birds, and the store of nutriment which it contains, serves only for the earliest period of the developmental process; but in the later stages of this process, the embryo draws for itself a continual supply from the circulating fluid of the parent, by means of a new and special apparatus; and after this has ceased, and it has come into the world alive, it is nourished for some time longer by the mammary secretion. The degree of development which the fœtus has attained at the time of its birth, however, varies considerably in the different orders, as does also the completeness of the apparatus by which the fœtus draws its nutriment from the parent; and hence is founded the division of the class into the two sub-classes of *Placental* and *Implacental* Mammals—the special apparatus for the nutrition of the fœtus of the latter never attaining the character of a true 'placenta,' and their whole organization presenting many points of affinity to that of the oviparous Vertebrata. Here, again, therefore, we have a marked illustration of the general conformity between the grade of development ultimately to be attained, and the degree and duration of the parental assistance early afforded to the embryo; and this is further manifest in the general correspondence which may be noticed, between the degree and duration of the dependence of the young animal upon its parent after birth, and the elevation of its subsequent condition. Those which are earliest able to obtain their own food and to keep up an independent temperature, make (for the most part) but little advance beyond that point; whilst the highest development of the cerebrum, and the most decided indications of intelligence, are met with among those whose

period of self-support is the longest postponed. In the case of Man, the prolongation of the period of infancy has a most important and evident influence upon the social economy of the race.

69. The class Mammalia, taken as a whole, is not characterized so much by the possession of any one particular faculty—like that which has been seen in Birds—as by the perfect combination of the different powers, which renders the animals belonging to it susceptible of a much greater variety of actions, than any others can perform. There are none that can compete with Birds in acuteness of sight; but there are few that do not possess the senses of smell, taste, and touch in a more elevated degree. There are none which can rival Birds in rapidity of locomotion; but there are few which cannot perform several kinds of progression. Their inferior energy of muscular movement is accompanied by an inferior amount of respiration; the type of the respiratory apparatus, however, is higher than in Birds, a like extent of surface being comprised within a smaller space. The lungs are confined to the cavity of the thorax; and there is a provision for the regular renewal of the air received into them, by the action of the diaphragm, which here completely separates that cavity from the abdomen. The diminished amount of respiration, again, involves the production of a lower degree of animal heat; so that the temperature of this class seldom rises above 100°. There is less need of means, therefore, for effectually confining their caloric —especially, too, as their greater average size causes their radiating surface to be much less in proportion to their bulk, than is that of Birds; and accordingly, we find them provided only with a covering of hair or fur, which is much less warm than that of feathers, and which is usually thin and scanty in Mammals inhabiting tropical climates. In the Cetacea, which are animals adapted to lead the life of Fishes, the same end is answered by the interposition of an immense quantity of oleaginous matter in the meshes of their enormously-thickened skin; thus forming the 'blubber,' which constitutes an admirable badly-conducting septum between the warm body of the animal it incloses and the cold water of the surrounding ocean.—The inferior nervo-muscular energy of Mammals as compared with Birds, renders it unnecessary that the nutritive functions in general should be carried-on with that extraordinary activity which characterizes the last-named class. Accordingly we find that the demand for food is less constant, the digestive process is less rapidly accomplished, and the circulation is slower, than in Birds; whilst on the other hand the 'waste' of the body, as indicated not merely by the amount of carbonic acid set free, but by that of the other *excreta* (especially the urinary), is less considerable, although the organs by which it is eliminated are developed (like the respiratory apparatus) upon a higher plan.

70. Although the skeleton of any ordinary four-footed Mammal presents a strong general resemblance to that of a Lizard, the mode of locomotion being the same in both cases, a considerable advance in the grade of development is observable, when the osseous framework is more closely examined. This is remarkably the case with regard to the intimate structure of the bones themselves, which are conformable to the Reptilian type (in the absence of any well-marked central cavity) at an early period of their evolution, but in which a dense shaft with a hollow

interior is afterwards substituted for the cancellated tissue which at first prevails throughout; and it is the case also with regard to the consolidation which the skeleton undergoes, by the gradual union of parts originally developed from distinct centres. The skeletons of the non-placental Mammals, however, present many interesting links of affinity to those of Reptiles; as do also those of the gigantic extinct Sloths, between which and the Dinosauria there seems to have been a mutual approximation.—The conformity of the different orders of Placental Mammals to one plan, as shown in the structure of their skeleton, is much greater than it is in Reptiles. We never find the extremities entirely suppressed, as in Serpents; nor are the ribs anywhere absent, as in Frogs; nor is there any such junction of the dermo-skeleton with the neuro-skeleton, as presents itself in the Turtles, although the former may constitute (as in the Armadillo) a complete bony envelope. Still, the modifications which do present themselves, are far more considerable than are exhibited by the class of Birds; and these have reference, as in Reptiles, to the adaptation of Mammals for residence in the water, like Fishes, or for passing a large part of their lives on the wing, like Birds. In the Cetacea, the power of locomotion is almost entirely taken away from the extremities, and given back to the trunk, as in Fishes, the posterior extremities being entirely deficient, whilst the anterior serve only for guidance; there is this important difference, however, that the tail, which is flattened vertically in Fishes, is flattened horizontally in Cetacea, which, being air-breathing animals, need the power of frequently coming to the surface to respire. In the Cheiroptera, on the other hand, the power of locomotion is almost entirely delegated to the anterior extremities, most of the bones of which are of large proportional dimensions, the principal elongation, however, being in the bones of the hand (Fig. 2, E); and their skeletons exhibit various other adaptive modifications for the same end, the sternum, for example, having a prominent keel, and the pelvis having its arch incomplete, as in Birds. But although the paddles of the Whale may *remind* us, in position and external aspect, of the pectoral fins of a Fish,—the rudimentary condition of the neck causing them to be situated just behind the head, and the inclusion of the short arm and fore-arm within the trunk leaving only the bones of the hand to support the undivided skin,—the essentially Mammalian type may be traced in all the parts of the skeleton of these members (Fig. 2, C); the only real approximation to a lower grade consisting in the multiplication of the phalangeal bones, as in the Enaliosauria, the digits themselves never exceeding their regular number five. The same constancy to the Mammalian type shows itself in the bones of the anterior extremity of the Bat; which, though modified for exactly the same purpose as that of the Bird (so that bats and swallows replace one another in the pursuit of the same insect-prey), attains that purpose by a different plan of organisation.

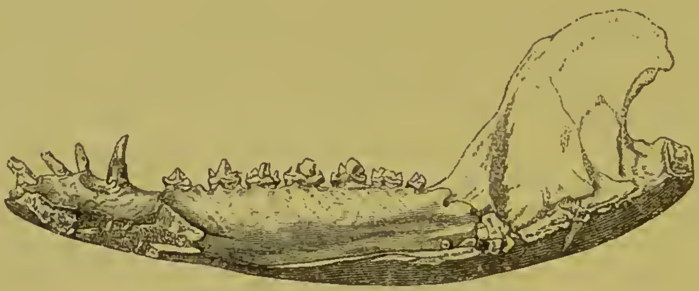
71. The following are the most important distinctive peculiarities in the skull of Mammalia. The cranial cavity, which is of a rounded form, is shut-in by a set of bones, which, while formed by the partial consolidation of the elements of the neural arches of the cranial vertebræ, remain separate during the whole of life, distinct sutures being interposed between them; the bones of the face are usually but little developed in proportion, save in certain tribes in which the skull is much elongated

in consequence of the great development of the jaws, and they are all (with the exception of the lower jaw) immovably articulated to each other and to the cranium; the lower jaw articulates directly with the cranium, instead of by an intermediate moveable tympanic bone as in oviparous Vertebrata, this piece having coalesced with other vertebral elements to form the 'temporal bone;' and the articulation of the cranium with the spinal column is no longer effected by the centrum of the occipital vertebra, but is formed by two lateral surfaces, corresponding with the articulating processes of ordinary vertebræ.—The number of cervical vertebræ is almost invariably 7; and this is not altered, either in the Cetacea, which have a very short and immovable neck, or in the Giraffe, whose neck is enormously elongated. The number of dorsal or rib-bearing vertebræ usually varies between 11 and 20; the ribs are always articulated, save in the most Reptilian Mammals, both by their 'heads' with the bodies of the vertebræ, and by their 'tubercles' with the transverse processes; the costal cartilages or sternal ribs usually remain cartilaginous, although they sometimes become ossified in advancing life; and they are for the most part undeveloped in Cetacea, the freedom of whose spinal ribs (with the exception of the first pair or two) reminds us of Fishes. The development of the sternum varies very considerably in different groups, chiefly in accordance with the demand for muscular power in the anterior extremity; thus it is not only in the Mole that it possesses a central projecting keel, but also in Moles and Armadilloes, whose fore-feet are used as spades in burrowing. It is not ordinarily prolonged over the abdomen, the abdominal sternum and ribs of Reptiles being represented only by longitudinal and transverse aponeurotic bands; but this portion is unusually developed in the Edentata. The ordinary number of lumbar vertebræ is either four or five; that of the sacral varies more considerably, the number of vertebral segments consolidated for the support of the pelvic arch, generally showing a proportion to the degree of strength which the members it bears are formed to exert. Thus in the Cetacea, which have no posterior extremities, the union of vertebræ into a sacrum is altogether wanting, as in Fishes; in Man and most of the higher Mammalia, on the other hand, five or even six vertebræ are consolidated: yet in the implacental Mammals, the Reptilian number two uniformly presents itself, notwithstanding that in many of them, as the Kangaroos and Opossums, the posterior extremities are enormously developed, and are the principal instruments in progression. The number and development of the caudal vertebræ vary more widely than do those of the segments of any other region; for whilst in Man and the higher Apes there are no more than 4 or 5, these being abortive and becoming anchylosed with each other so as to form the 'os coccygis,' the number rises (in other Mammalia) to 20, 30, or even 40. It is interesting to remark that the highest numbers occur in those orders (the Marsupialia and the Edentata) which present the greatest number of other approximations to the Reptilian type of structure; and in some of the former of these, we find a very curious reversion to the Reptilian type, in the presence of hæmal arches attached to the bodies of the caudal vertebræ. As a general fact, however, the tail is a part of the vertebral column, whose development or non-development does not follow any general plan, but is related to the special use to be made of it in the economy of the animal; and of such uses the Mammalian class presents a remarkable variety. The conformation of the scapular arch in Mammals generally differs from that of Oviparous Vertebrata in the inferior development of the coracoid element, which is not of sufficient length to reach the sternum or to meet its fellow on the median line; the osseous connection of the scapula with the sternum, where such exists, being established by the clavicle. In the Monotremata, however, with other reptilian affinities, we find this connection to be established both by coracoid and clavicle in a most peculiar manner, through the intermediation of an 'episternal' bone; the whole clavicular arch having a most remarkable resemblance to that of Ichthyosaurus. The three component bones of the pelvic arch generally coalesce together at an early period of life, remaining separate, however, in Monotremata; the inferior symphysis is complete (save in Bats), being entirely formed by the junction of the rami of the pubis; but in the Implacentalia, as in Reptiles, the ischia have a share in the junction. The extremities attached to these arches exhibit a great variety of special modifications of structure; putting aside, however, the extreme modifications presented in Bats and Whales, we recognize two principal sub-types, the *ungulated* and the *unguiculated*. In the former of these (Fig. 2, D), the members, being adapted simply for support and locomotion, are developed in a form which renders them most efficient instruments for these purposes. All the articulations, even those of the shoulder and hip-joints, are so constructed as to limit the movements of the limb to that one plane (backwards and forwards) in which its actions are required for the onward propulsion of the body; the bones of the fore-arm and leg are consolidated into one, so as entirely to prevent any rotation of the hand or foot; and only a pair of digits, or even a single one, are developed in each member, these being entirely enveloped in hard horny casings. The opposite extreme is where, as in Man (Fig. 2, F), the form of the humeral articulation, and the arrangement of its muscles, confer upon the anterior extremity (the posterior partaking of the same endowments, but in an inferior degree), the power of free and extensive motion; the plane of the hand can be turned in any direction by the rotation of the fore-arm and the flexure of the wrist; the whole number of digits is developed, and one of them is so opposed to the rest as to be capable of antagonism to either one or to all of them collectively; and the extremities of the fingers are covered by the nail on one side only, leaving the other possessed of the highest tactile delicacy. Between these two extremes, there is an immense variety of intermediate gradations.

72. The teeth of Mammalia constitute a remarkably characteristic feature in their organization; and the differentiation which they exhibit in the several orders and genera is so great, and is so closely connected with other peculiarities, as to afford most important assistance in classification. They are, for the most part, much less multiplied than in Reptiles; and when the typical number 44 is exceeded, it is in those groups which either represent Fishes, or make the closest approximation to Reptiles; and it is in these, moreover, that the teeth, having the least degree of individual development, present so little differentiation, that they cannot be classed, as they may be in all the higher forms of the dental

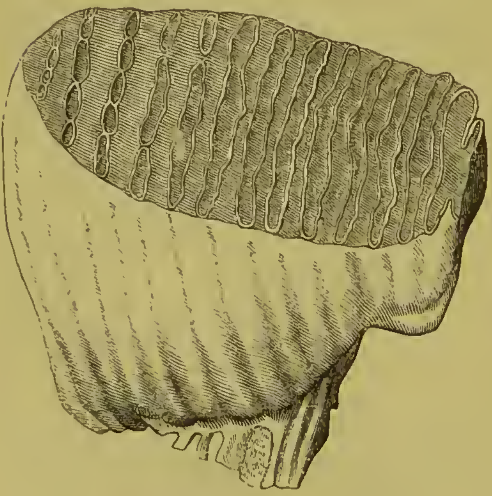
apparatus, into *incisors, canines, premolars,* and *molars.*—In the mode of implantation of the teeth of Mammalia, we have a marked distinctive character of the class; for in all save those which grow from persistent pulps, we find the dental cavity closed-in at its lower part, and the base of the tooth prolonged into a 'fang,' which is implanted into its own proper socket, but not united by ossification to its bony wall. The fang of molar teeth is usually subdivided into two, three, or even four portions, which diverge more or less from each other, and are received into separate divisions of the alveolar cavity; and this mode of implantation is so peculiar to Mammals (as far as at present known), that its existence appears sufficient to determine the mammalian nature of a jaw, or even of a fragment of a jaw, in which it occurs, such as that of *Phascolotherium* (Fig. 71), or *Amphitherium,* of the Stonesfield slate, whose reptilian nature has been advocated by many zoologists.—The teeth of Mammalia are ordinarily cast and renewed but once during life, instead of being continually shed as they are in Reptiles and Fishes, and replaced by new teeth developed from independent papillæ, or from offsets from the previous follicles. This general rule, however, is subject to exceptions in particular cases. For in the Elephant, we find the sides of the jaws to be occupied, not by rows of molar teeth, but by a single large composite tooth on either side of each jaw (Fig. 72), this being formed of a succession of alternating plates of enamel, cementum and dentine. The chief wear of these teeth is in front; and a production of new teeth is continually taking place behind, so that each tooth, as it wears down, is pushed forward by the new tooth behind it, which comes to occupy its place; and the molars are thus changed six or eight times. The 'tusks,'

FIG. 71.



Lower jaw of *Phascolotherium Bucklandii.*

FIG. 72.



Molar tooth of *Asiatic Elephant.*

on the other hand, though only renewed once, like the teeth of Mammals generally, are in a state of constant growth from the persistent pulps at their base; and this plan is adopted also in several other cases, in which the teeth are particularly liable to be worn-down by the friction to which they are exposed.

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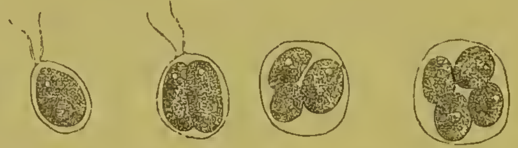
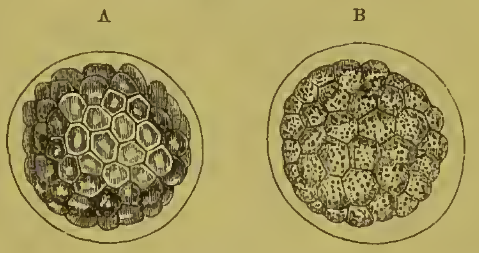
73. Having thus found, in the general survey we have taken of the Vegetable and Animal kingdoms, that the 'idea' of their combined unity and diversity of organization is that of progress *from the more general to the more special,* we shall enquire how far that idea is conformable to the actual history of their Development. This, when carefully scrutinized, is found to afford the most satisfactory proof of it.—The perfect organism of any one among the higher Plants and Animals is not more dissimilar in form and condition to that of the lowest and simplest member of either kingdom, than it is to the germ of its own kind in the earliest periods of its evolution; and in fact, when we go back to the very commencement of the process, we observe that the *most general* type of organised structure,—the simple cell,—is that in which every living being commences. The evolution of the germ commences in the duplicative multiplication of this cell, precisely after the fashion of the multiplication of the simplest Protophyta and Protozoa (Fig. 73). It is not until this has proceeded to a considerable extent, that it could be stated with certainty, from the appearance of the germ alone, whether it is that of a Plant or of an Animal; thus in the accompanying figure (Fig. 74), the 'mulberry-mass' of the mammalian ovum, formed by the repetition of the duplicative subdivision of the germ-cell, is shown to bear a most exact correspondence to the *Volvox globator* (an organism now certainly known to belong to the vegetable kingdom) in its early stage. At the time, again, when the distinctive characters of *animality* first present themselves, it could not be predicated whether the germ is that of a Radiated, Molluscous, Articulated, or Vertebrated animal; the special characters of these sub-kingdoms not being evolved until a later period. These, however, are the next to appear, but still the distinctive peculiarities of the class are wanting; the germ of a Vertebrated animal (for example) being at first destitute of anything that can mark it out as a Fish, Reptile, Bird, or Mammal. When the distinctive characters of the class have been made manifest by the further progress of development, those of the order still remain indeterminate; these are evolved in *their* turn; and then those of the family,

FIG. 73.



Multiplication of cells of *Chlamydomonas* (Ehrenb.) by duplicative subdivision.

FIG. 74.



A, early stage of *Mammalian Ovum*;—B, young of *Volvox Globator.*

genus, species, sex, and individual, in succession.* This, at least, is the result of observations made in a considerable number of cases; and where such an accordance does not exist, the want of it is probably due to imperfections in the system of classification with which the comparison is made.—Thus we see that in watching the history of the development of any one of the higher forms of organised structure, we find the realization of that ideal evolution of *the more special characters from the more general,* which it is the object of the Philosophic Naturalist to bring into view by the methods of proceeding already pointed out (§ 11).

74. The general principle of Von Baer affords the real explanation of those resemblances which are sometimes discernible, between the transitory forms exhibited by the embryoes of higher beings, and the permanent conditions of the lower. When these resemblances were first observed in the study of Embryology, an attempt was made to generalize them in the statement "that the higher animals, in the progress of their development, pass through a series of forms corresponding with those that remain permanent in the lower parts of the animal scale." But this statement was hasty and unphilosophical; and it is now only referred-to, for the sake of showing what amount of real truth there is in it.—No animal *as a whole* passes through any such series of changes, except where it comes forth from the egg in an early stage of development, but in a condition that enables it to sustain its own existence, and to lead the life of a class below, from which it is afterwards raised by metamorphosis. This is the case, for example, with such Insects as resemble Annelida in their larva condition, and with Batrachian Reptiles, which are essentially Fish during the early period of their lives. But in neither of these instances, does the Larva entirely resemble the *perfect* animal which it represents in form and grade of organisation; for besides having its generative system undeveloped (without which it cannot be said to be a complete animal), the condition of its tissues and organs is altogether embryonic; so that the caterpillar bears a much closer accordance with the embryonic than with the adult Annelide, while the Tadpole is more nearly related to the embryonic than to the perfected Fish. These and other cases of the same kind must be regarded as special modifications of the general plan to meet a particular purpose; and while they present nothing discordant with that plan, they cannot be taken as examples of the usual mode in which it is followed out. On studying the development of any one of the higher animals, which remains within the ovum until it has attained the form characteristic of its class, we find that its entire structure does *not* present at any time such a resemblance to either of the classes beneath, as would

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* Although this general truth had been previously indicated by Von Baer, yet the first definite and complete statement of it, with its application to Classification, will be found (the Author believes) in two papers 'On Unity of Structure in the Animal Kingdom' contributed by Dr. Martin Barry to the "Edinburgh Philosophical Journal" for 1837. It has been subsequently developed in a very admirable manner by Prof. Milne-Edwards in a Memoir 'On the Principles of the Natural Classification of Animals,' in the "Annales des Sciences Naturelles," Ser. III., tom. i., which bears evidence of having been written without the knowledge of what either Von Baer or Dr. Barry had put forth; the principle, in fact, having been advanced in a more limited form by Prof. Milne-Edwards himself, in a memoir 'On the Changes of Form exhibited by various Crustacea during their Development,' read by him to the French Academy in 1833, and published in the "Annales des Sciences Naturelles," Ser. I., tom. xxx., Ser. II., tom. iii.

justify the slightest analogy; thus, the Human embryo is never comparable with a Fish, a Reptile, or a Bird, much less with an Insect or with a Mollusk. In its very earliest grade, indeed, it might be likened to the cells, or clusters of cells, of which the *Protophyta* and *Protozoa* are constituted (Fig. 73, 74); but so soon as the multiplication and conversion of these has proceeded to such an extent, as to give it a form and structure in which a resemblance can be traced to *any* higher animal, it is to the Vertebrated type that we should at once assign it. Now, whilst it is passing through this condition, a close correspondence may be traced between the several parts of *its* structure and those of *any other* vertebrated embryo at a similar grade of development:—there is, for example, no essential difference between the vertebral column of the early embryo of Man, and that of an embryo Fish; the evolution of the nervous centres begins in both upon the same plan; so also does that of the circulating apparatus. And as the progress of development is arrested in the lower tribes, at the stages thus indicated in the transitional conditions of the higher, a mutual resemblance in the condition of particular organs may most assuredly hence arise. Thus, in the Cyclostome and higher Cartilaginous Fishes, we find permanently represented the various stages in the development of the vertebral column, which may be detected in the embryo of higher Vertebrata. But each of these animals presents, in its adult condition, a special adaptation of the general plan to its own organism; and this special modification is *not* represented in the human embryo. Thus, whilst the cranium of the Human embryo is developed from a great number of distinct centres, which represent the bones that remain permanently separate in the skull of the Fish,—so that there is a correspondence in the condition or grade of development, as presented in the two cases respectively,—yet it never exhibits those peculiar characters, which distinguish the skull of the Fish from that of all other Vertebrata. Or, to take an illustration from another source, the Circulation is carried on, at an early period in the development of all vertebrated animals, by a system of blood-vessels distributed upon the same plan as that which is met-with in the adult Fish. It is not, however, correct to affirm, that the circulating apparatus of Man ever passes through the condition of that of a Fish; for although the 'branchial arches' are developed in *all* Vertebrated animals, so that their presence may be considered as the *most general* fact in the history of their arterial system, yet the twigs which they give off in the adult Fish for the supply of the branchial filaments are never developed, except in animals that are to be adapted for aquatic respiration; so that the blood flows onwards continuously through the branchial arches, and is delivered by them into the aorta, instead of being distributed amongst the gills, to be returned from them by a distinct set of vessels, the branchial veins. Hence, however close may be the resemblance between the *embryo* Man and the *embryo* Fish, there is no real correspondence between the *embryo* of Man and the *completed* Fish; since every departure from the general plan or 'archetype,' which gives to the embryo Fish the special characteristics of its class, does in reality diminish the resemblance borne to it by the embryo of either of the higher classes. Thus, whilst there is at an early period a very close correspondence between the embryoes of all classes of Vertebrata, in harmony with the general principle of Von Baer, each one of these, as it proceeds in its course of development, takes a direction that separates it from the rest; and the mutual divergence consequently becomes greater and greater, in proportion as the perfected form and condition, that are characteristic of each class respectively, are approximated.

75. Now although the life of all Organised beings commences in the simplest and most general type of organic structure, so that there is no perceptible distinction between their germs, yet we see that each germ must have a certain capacity of development peculiar to itself; since it is a general law of Organic Development, that *like produces like.* However varied may be the series of forms through which the parent passes, the offspring repeats these with the greatest exactness;* and the whole scheme of development may be described as one in which the primordial cell is tending towards the attainment of the perfect form and condition of its parent. In proportion to the mutual resemblance of the parents, will be the conformity of the processes by which their respective forms are attained; in proportion to the dissimilarity of their adult conditions, will be the divergence of their directions of development: thus the development of the heart of the Bird and of the Mammal proceeds upon a method essentially the same, the single ventricle being divided first, and the single auricle subsequently, the septum remaining imperfect in the Mammal until birth; but in the Reptile the auricle is first divided, its circulation being carried-on upon a plan to which the embryo Bird and Mammal never present anything comparable. And in accordance with the degree of proximity of each complete form to the general model or 'archetype' of the entire series, will be the degree in which it will be represented in the transitional states of the higher forms: thus the vertebral skeleton of the Fish as a whole departs much less from the archetype, than does that of the Bird; and consequently, that of the embryo Mammal is much more nearly related to the former, than it ever is to the latter.—These examples will serve, it is hoped, to show the distinction between the fundamental principle of development, first enunciated by Von Baer, and which is applicable (as the author believes) to all the facts hitherto ascertained, and that crude and illogical generalization which has brought discredit upon Philosophical Biology, and has led to a host of erroneous inferences.†

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* It will be shown hereafter (CHAP. XI.) that the phenomena ranked under the term 'Alternation of Generations' do not constitute a real exception to this rule.

† It is owing to the ignorance of Von Baer's writings which has generally prevailed in this country, that the credit has been recently assigned to others, of having first enunciated the true view of this subject. The Author may refer to the second edition of the present work, published in 1841, as having contained the doctrine stated above, which he was also accustomed to teach in his Physiological Lectures; and although his own acquaintance with Von Baer's works at that time extended but little beyond the references made to them by Dr. Martin Barry, yet these were sufficient to enable him to comprehend and apply the great developmental law which Von Baer had so clearly enunciated, and to lead him to the very same illustrations as those which he afterwards found that Von Baer had employed. He cannot but think that the admirers of the great English comparative anatomist of our own time, would have done well to abstain from preferring on his behalf any claim to originality on this subject, until they had ascertained how far he had been anticipated by others. In the "Quarterly Review" for October, 1851 (vol. lxxxix. p. 430), Prof. Owen is spoken of as having "first distinctly enunciated the generalization, that in the development of the vertebrate animal, the germ passes at once from the common form of the protozoon or monad to the vertebrated type, without transitorily representing either the radiate, articulate, or molluscous types." Now in Von Baer's great work "Uber Entwickelungs-Geschichte

76. It is maintained, indeed, by some distinguished Naturalists, that the information derivable from the history of Development, in regard to the relative value of characters and the affinity of groups, is so much more certain and satisfactory than that of any other kind, that it ought to furnish the fundamental data for a truly scientific classification; those tribes being considered as most nearly related to each other, whose embryonic development advances furthest along the same course without divergence; whilst those are to be regarded as most fundamentally dissimilar, whose directions of development are distinct from the earliest period. This principle may be admitted as one which deserves to be fully taken into account, in any attempt at a systematic arrangement on philosophical principles; but to adopt it to the exclusion of all comparison of forms in their state of complete evolution, would be to deprive important changes which may occur at a comparatively late period of development, of their due claim to consideration. The following illustrative examples may help to make its true value apparent.—In the class of *Crustacea,* as long since observed by Prof. Milne-Edwards, the young of such as come forth from the egg at an early period of development, and have many changes to undergo, resemble one another very closely. As they increase in size, however, the peculiarities of the respective tribes to which they may belong, gradually manifest themselves, partly through an alteration in the rate of development of different parts, and partly by the evolution of new and special organs. Thus in one case, it is the thorax which grows more rapidly than the abdomen, and greatly preponderates; in another, it is the abdomen which presents the greatest increase in its dimensions; in other instances, again, an extraordinary development is seen in certain extremities, or even in certain articulations of these extremities. So, again, it is not uncommon for certain parts which were possessed by the embryo Crustacean, to become atrophied and to disappear; thus still further tending to *specialize* the particular form in its progress towards its complete development. In these and other modes, the larva, which, at the time of its emersion from the egg, may have presented no characters that serve to distinguish it from the larvæ of numerous other very dissimilar forms, gradually comes to present in succession the characters of its tribe, genus, species, and sex.* A very good example of this kind of specialization is afforded by certain parasitic Crustacea of the Entomostracous group; which have their forms so altered by the enormous development of their ovaries (Fig. 75, B, *a, a*), as well as by the evolution of egg-sacs (*b, b*), and by the modification of their appendages for adhesion and of their mouth for suction, that they were long ranked in a distinct group, under the designation of *Epizoa,* their original type being almost obliterated. Yet it is now known that

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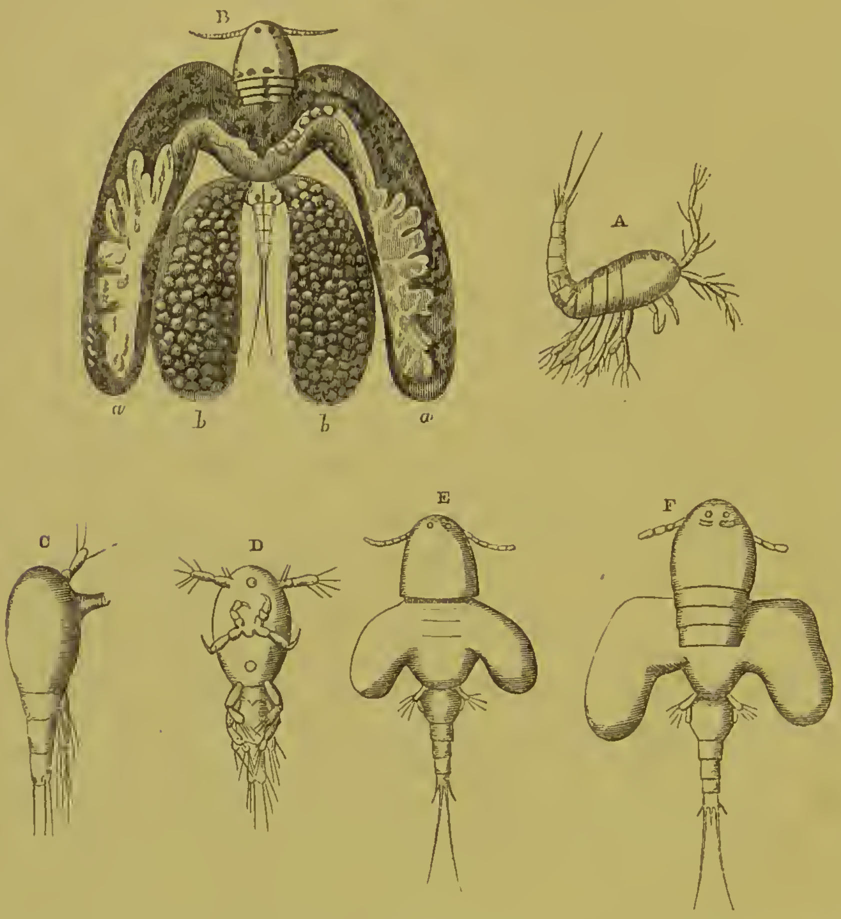
der Thiere," 1828, the enunciation and proof of this very doctrine occupy the 4th section of his 5th Scholium. At that period, it is true, the relation of the earliest states of the embryonic mass, with the permanent conditions of the Protozoa, had not been detected; but that the *chorda dorsalis,* the most characteristic feature of the Vertebrate embryo, is the first part that is differentiated, and that the vertebrate embryo never bears the slightest correspondence to the special radiate, articulate, or molluscous types, is over and over again *most emphatically asserted.*

* See the Memoir of Prof. Milne-Edwards already cited; also his "Histoire des Crustacés," and his article *Crustacea* in the "Cyclopædia of Anatomy and Physiology," vol. i.

this modification is exhibited by the females alone; the males (A), which are often so small as to be mistaken for parasites upon the female, continuing to exhibit the ordinary Entomostracous type, that of Nicothoe bearing a close resemblance to Cyclops (Fig. 60); and the change in the female only taking place gradually, as her generative apparatus evolves itself (C, D, E, F).*—If we turn, on the other hand, to the *Cirrhipeds*, we find that whilst they closely agree with Crustacea in their larval condition, and must, if the principle of development be followed as the sole guide, be placed at no great distance from the Entomostracous subclass, if not as actual members of it, they undergo such extraordinary metamorphoses at a later stage, that their character is changed in a degree sufficient to exclude them from any definition, however comprehensive, which may be framed for that class; whilst they are brought into much closer approximation with the Mollusca, than is exhibited by any other group of the Articulated series (§ 14).

FIG. 75.



A, male of *Nicothœ astaci*:—B, adult female of the same species, having two large lateral appendages, *a*, *a*, containing the ovaries, as well as two egg-sacs, *b*, *b*;—C, young larva viewed sideways;—D, more advanced larva, provided with all its members;—E, larva already fixed, the lateral appendages beginning to appear;—F, further development of the same.

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* Van Beneden 'Sur le Développement et l'Organization des Nicothoés,' in "Ann. des Sci. Nat.' 3ième Serie, Zool., tom. xiii., p. 354, *et seq.*

77. Thus, then, whether we compare the whole assemblage of perfected forms which make-up any one group, or examine into the progressive changes which they respectively undergo in attaining their complete development, we find that their differences essentially consist in the relative development of the elements which all possess in common. Hence, as Prof. Bell remarks with special reference to the Crustacea,* we arrive at the great economical principle, that *the typical structure of any group being given, the different habits of its component species or minor groups are provided for, not by the creation of new organs or the destruction of others, but by the modification in form, structure, or place, of organs typically belonging to the group.*—Thus the proboscis of the Elephant, which constitutes so wonderful an instrument of prehension, is but an extended nose; and an approach to a like extension is presented by the Tapirs among existing Mammals, as well as (judging by the conformation of the cranium) by various extinct Pachydermata. The wing of the Bat, as we have seen, is not an additional member, but is stretched upon an extended hand; that of the Pterodactylus, upon a single finger. The neck of the Giraffe contains no additional vertebræ; but is adapted to its offices by peculiar modifications in the structure of the limited number typical of the Mammalian class. So, the protective shield of the Turtles is not so complete an *addition* as it would at first appear, to the ordinary skeleton of the Reptile; nor in the horny mandibles which cover its jaws, have we an organ which is altogether new to the group, since these are formed by a different development of the same elements as those from which teeth are elsewhere produced.—So, turning to the Vegetable kingdom, we find that special organs, such as tendrils, pitchers, fly-traps, &c. are evolved out of the more general type of the leaf, and are not introduced as additions to the ordinary fabric.

78. Again, we find, as might have been expected under the foregoing law, that if the plan of structure in a particular tribe involves the *non*-development of some organ which is possessed by neighbouring groups, its conformity to archetypal regularity is generally manifested by the presence of that organ in a *rudimentary* or undeveloped condition. Thus, we find some rudiment of the lung in most Fishes, even where it is not sufficiently developed to serve as an 'air-bladder' in regulating the specific gravity of the body. In the abdominal muscles of Mammals, again, we find the abdominal sternum and ribs of Saurian Reptiles indicated by white fibrous bands; and in those Mammals which do not possess a clavicle, that bone is usually represented by a ligament, just as the stylo-hyoid ligament in Man represents a portion of the hyoidean arch which is elsewhere completely ossified. Such rudimentary structures, however, often display themselves only at an early period of development, and are subsequently lost sight of. Thus the rudiments of teeth, which are never developed, and which at a later period cannot be detected, are found in the embryo of the Whale, both in the upper and under jaws; and Prof. Goodsir has ascertained that the rudiments of canine teeth, and of the incisors of the upper jaw, which are not subsequently developed, exist in the embryoes of Ruminating Mammals.†

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* "British Crustacea," Introd. p. xiii.

† "Report of the British Association," 1839, p. 82.

The most remarkable example of this kind, however, is the existence of *branchial arches,* resembling those of the Fish, in the early embryo of *all* air-breathing Mammalia, as will be hereafter explained (CHAP. VI.).—The same is true, as a general rule, in the Vegetable kingdom; thus when a whorl or part of a whorl in a flower is suppressed, the deficiency is manifested, either by the presence of the undeveloped organs in a rudimentary form, or by the leaving of a space for them (so to speak) in the arrangement of the parts which are present. Thus in the *Primrose* tribe, we commonly find a single row of stamens *opposite* to the petals, instead of *alternating* with them, according to the regular plan of floral development (§ 30); and hence the Botanist would conclude that a whorl has been here suppressed, which ought to intervene between the petals and the stamens. This is found to be the case in the genus *Samolus,* whose flower, formed in other respects upon the same type with the Primrose, possesses the rudiments of the intermediate row, in the form of a whorl of little scales, not developed into stamens. In the common *Sage,* again, we find only two stamens, where the general plan of the flower would lead us to expect five; but upon looking attentively at the interior of the corolla, two little scales are often to be seen growing in the place where two of the deficient stamens should have been; these two scales are frequently developed as perfect stamens, in flowers which are otherwise constructed precisely like the Sage; and even the fifth makes its appearance in some instances, exactly where it should be regularly found. Sometimes, again, the conformity to a common type is manifested by the full development, under cultivation, of organs which are not usually evolved: thus there are plants in which one set of flowers is purely 'staminiferous,' from the non-development of the carpellary whorl, whilst another set is 'pistilline' only, from the non-development of the stamens; and in which the effect of increased nutriment is to develope the deficient carpels in one set, and the deficient stamens in the other, so as to render both of them complete and 'hermaphrodite.'

79. The attempt has been made to bring the diversities in the proportional development of organs which different animals possess in common, under a general expression,—*the balancing of organs;*—which is nothing else than that which is alluded-to by Paley and other authors, as the "principle of compensation." This has been stated in the following most objectionable form:—that the extraordinary development of one organ *occasions* a corresponding deficiency in another, and *vice versâ.* It is perfectly true that, in a great majority of cases, *the extraordinary development of one organ is accompanied by a corresponding deficiency of development in another;* but the development and the deficiency are both of them parts of one general plan, and neither can be regarded as the cause, or as the effect, of the other. Thus, in the Human Cranium, the elements which form the covering or protection of the brain are very largely developed, whilst those which constitute the face are comparatively small. In the long-snouted Herbivorous Mammals, as in Reptiles and Fishes, on the other hand, the great development of the bones of the face is coincident with a very small capacity of the cerebral cavity. In the Bat, whilst the anterior extremity is widely extended, so as to afford to the animal the means of rising in the air, the posterior is very much lightened, so as not to impede its flight. In the Kangaroo, on the other hand, the posterior

members are very large and powerful, enabling the animal to take long leaps; whilst the fore paws are proportionally small. The Mole, again, requires for its underground burrows the power of excavating with its fore-feet, whilst the hind legs are used for propulsion only; and the relative development of these members follows the same proportion as in the Bat, although the *plan* in the two cases is widely different. Moreover it is obvious that, from the peculiar habits of this animal, eyes would be of little or no use to it; and accordingly we find them merely rudimentary, and no cavity in the skull for their reception; whilst to compensate for the want of them, the organ of smell, and its capsule—the ethmoid bone, are amazingly developed. In other classes of animals, similar illustrations abound; thus, the Birds of most active and energetic flight usually have the smallest and feeblest legs; and the Struthious birds, in which the legs are enormously developed, have only rudimentary wings. So, again, among Reptiles, we find the vertebral column most lengthened, and the tail especially developed, in those whose limbs are feeblest, or altogether deficient, as among Serpents, and Serpent-like Sauria and Batrachia; whilst, if the limbs are the principal instruments of locomotion, as in Frogs and Turtles, the vertebral column is shortened, and the tail contracted. And in Fishes, the same general rule holds good.—In no class, however, is this rule without its exceptions; and it must be taken rather as an expression of facts, possessing a certain *empirical* value, than as entitled to the character of a 'law' of development, which some would claim for it.

80. Another principle, propounded by Cuvier, and supported by those who have adopted the 'functional' or 'teleological' (purposive) rather than the 'homological' relations of organs as their guide, is that of the *harmony of forms*, or the *coexistence of elements*. It implies that there is a necessity, arising out of the conditions of organic existence, for the combination of organs according to their several actions; that there is a constant harmony between organs which are functionally connected; and that the altered form of one is invariably attended with a corresponding alteration in the others. A general comparison of the skeleton of a Carnivorous with that of an Herbivorous quadruped, will furnish a characteristic illustration of this doctrine. The Tiger, for example, is furnished with a cranial cavity of considerable dimensions, in order that the size of the brain may correspond with the degree of intellect which the habits of the animal require. The face is short, so that the power of the muscles which move the head may be advantageously applied. The canine teeth are large and pointed; whilst the molars have sharp edges, adapted only for cutting, to which purpose they are most effectively applied by the scissors-like action of the jaw. The lower jaw is short, and the cavity in which its condyle works is deep and narrow, allowing no motion but that of opening and shutting; the fossa in which the temporal muscle is embedded, is very large; and the muscle itself is attached to the jaw in such a manner as to apply the power most advantageously to the resistance. The spinous processes of the vertebræ of the back and neck are very strong and prominent, giving attachment to powerful muscles for raising the head, so as to enable the animal to carry off his prey. The bones of the extremities are disposed in such a manner, as to allow the union of strength with freedom of motion; the head of the humerus is

round, and the articular surfaces of the fore-arm indicate that it possesses the power of pronation and supination. The toes are separate, and armed with claws, which are retracted when not in use by a special apparatus that leaves its mark upon the bones.—On the other hand, in the conformation of the Herbivorous quadruped, we are at first struck by the diminished capacity of the cranium, and the increased size of the bones of the face. The jaws are long, and the lower jaw has a great degree of lateral motion, the glenoid cavity being broad and shallow; and whilst the pterygoid fossa, in which the muscles that *rotate* it are lodged, is of large size, the temporal fossa is comparatively small, no powerful *biting* motions being required by the nature of the food or the mode of obtaining it. The front teeth are fewer and smaller; but the surfaces of the grinding teeth are extended, and are kept constantly rough by the alternation of dentine and enamel. The limbs are more solidly formed, and have but little freedom of motion, the hip and shoulder being scarcely more than hinge-joints; the extremities are encased in hoofs, which are double if the animal ruminates, and either single or multiple if it does not. The whole body is heavier in proportion, the nutritive system being more complicated; and the muscles which enable the tiger to lift considerable weights in his mouth, are here necessary to support the weight of the head itself.

81. That this statement is true so far as it goes, no one can deny; and the researches which have been based upon it have been most successful in repeopling the globe, as it were, with the forms of animals which have long been extinct, but which can be certainly predicated even from minute fragments of them. A little consideration, however, will show that the existence of such adaptations of parts is nothing more than a result of the general plan of development, and gives us no information of the nature of that plan. It is evident that, if it were deficient, the race must speedily become extinct, the conditions of its existence being no longer fulfilled; and that whatever be the laws of development, they must operate to this end, in order that the world may be peopled with life. An animal with the carnivorous propensity of the Tiger, for instance, and the teeth or hoofs of a Horse, could not remain alive from the want of power to obtain and prepare its aliment; nor would a horse be the better for the long canine teeth of the tiger, which would prevent the grinding motion of his jaws required for the trituration of the food.—The statement above given cannot, therefore, be regarded as a *law;* since it is nothing more than the expression, in an altered form, of the fact, that as the life of an organised being consists in the performance of a series of actions, which are dependent upon one another, and are all directed to the same end, whatever seriously interferes with any of these actions must be incompatible with the maintenance of its existence. The splendid discoveries of Cuvier and other anatomists, who have succeeded in determining, from minute fragments of bones, the characters of so many extraordinary species of remote epochs, have resulted from the sagacious appreciation of this truth, and from the use made of it in the laborious comparison of these remains with the similar parts of animals now existing. Until that comprehensive Plan shall have been discovered, of which these are so many individual manifestations, no briefer process can be adopted.

82. The tendency to conformity to an ideal 'archetype' is frequently shown, in a most remarkable manner, by the occurrence of *Monstrosities;* which, though once regarded by men of science with feelings very little higher than those with which they are still looked-on by the vulgar, may now be considered as among the most interesting and suggestive of all the illustrations of 'Unity of Design;' since of these malformations, a considerable proportion are such in virtue of their closer conformity to the *general* model, those modifications of it which are characteristic of the *special* form not having been evolved. Some of the most curious examples of this are furnished by the Vegetable kingdom.—Thus, the families *Lamiaceæ* and *Scrophularineæ* are distinguished by that peculiar form of corolla which is denominated *labiate,* from the two large lips bounding its mouth; and the stamens, instead of being five (like the sepals of the calyx), are only four in number, and are 'didynamous,' that is, two are longer than the other two. Now in these points, there is a departure from that symmetrical arrangement, and that equality of parts, which are characteristic of the *regular* flower; this departure being a modification special to the order, superinduced upon the more general type. A further modification is seen in certain genera of the *Scrophularineæ,* such as the common *Antirrhinum* (Snapdragon), in which a long spur is developed from *one* only of the petals of the corolla, whilst the upper lip is developed in such a manner as to form an arch, against which the lower lip closes completely, forming what is termed a *ringent* corolla. Now in cultivated specimens of this plant, it is not uncommon to meet with a reversion to the regular type; the petals being all equal and similar, so as to produce a circularly-symmetrical corolla, and each of them having a spur developed from its under side; while the stamens are augmented to five in number, and are all of equal length. So, again, in the common *Tropæolum* (Nasturtium), which in its normal state possesses one spurred petal, the tendency to regularity is exhibited, sometimes in the disappearance of the spur, sometimes in the development of the same appendage from other petals. The breaking-up of the whorls of a flower by the development of the internodes, so that its parts are found to be disposed in a regular spiral round the axis (which may be occasionally seen in the double Tulip and in some of the Euphorbiaceæ), is an example of reversion to a still more general plan, of which the flower itself is a special modification; and the same may be said of that reversion of each of the parts of the flower to the foliaceous type, which is sometimes witnessed in a single whorl, sometimes in the whole flower at once (§ 30).—In the Animal kingdom it is not difficult to trace the same tendency; the departures from the normal type, however, being for the most part greater in internal structure than in external conformation. Of the former kind, some of the most interesting are those which will be hereafter described as presenting themselves in the Circulating apparatus (CHAP. V.); of the latter, the most frequent (as among Plants) are those which occur in the generative system. For example, among the higher Mammals, in which the *specialization* of the sexual apparatus is the greatest,—that is, in which the differences of the male and female organs are most strongly marked,—it is not at all uncommon to meet with instances of 'spurious hermaphrodism,' which are really nothing else than approximations to the community of type that is seen transiently in

an early stage of their development, and permanently in those lower tribes, whose external generative organs are nearly alike in the two sexes. Thus in an animal whose general characters are those of the male, we may find the penis imperfectly developed, and not perforated by the urethra, which terminates in uro-genital fissure that opens posteriorly; and the two halves of the scrotum, separated by this fissure, may resemble the labia of the female, the testes not having descended to occupy them. On the other hand, in an animal in which the characters of the female on the whole predominate, the upper part of the vaginal canal may be closed, so that it cannot be distinguished from the uro-genital fissure found in an imperfect male; the clitoris is sometimes developed to a very large size, and the urethra may be continued to its extremity, either as a complete canal, or as a groove; and the ovaries, descending into the labia, may give them the character of a divided scrotum.

83. The 'idea' of progress from the more general to the more special, which we have thus found to prevail alike in the completed structure of the existing types of Vegetable and Animal organization, and in the developmental process by which they attain it, may also be traced in that long series of organic forms which have successively appeared and disappeared on the face of this globe, and have finally given place to those of our own epoch. The entombment of the remains of many of these, in the strata in progress of formation at the time of their existence, has enabled the Palæontologist to reconstruct, to a certain extent, the Fauna and Flora of each of those great epochs in the Earth's history, which are distinctly marked-out in Geological time, both by extensive disturbances in the earth's crust, and by striking changes in the structure and distribution of the living beings which dwelt upon it. Each of these epochs was characterized by some peculiar forms, or combinations of forms, of Animal and Vegetable life, which existed in it alone; and the farther we go back from the existing period, the wider are the diversities which we encounter, both in that general aspect of these kingdoms of nature which depends upon the relative proportions of their different subordinate groups, and in the features and structure of the beings composing these groups. The attempt has been made to prove, that these changes might be reduced to a law of 'progressive development;' meaning by this, that the lowest forms of Vegetable and Animal life were first introduced, that those of the least degree of elevation next presented themselves, and so on consecutively, until we reach Man, who, as the highest in the series, was the last to make his appearance upon the globe. Further, it has even been surmised that an actual 'transmutation' of the lower forms into the higher took place in the course of geological time; so that, from the germs first introduced, or from others which have since originated in combinations of inorganic matter, the whole succession of organic forms, from the simplest Protophyte up to the Oak or Palm, from the Protozoon up to Man, has been gradually evolved; not, however, in a single series, but from several distinct *stirpes* whose development has taken different directions.* The facts of Geolo-

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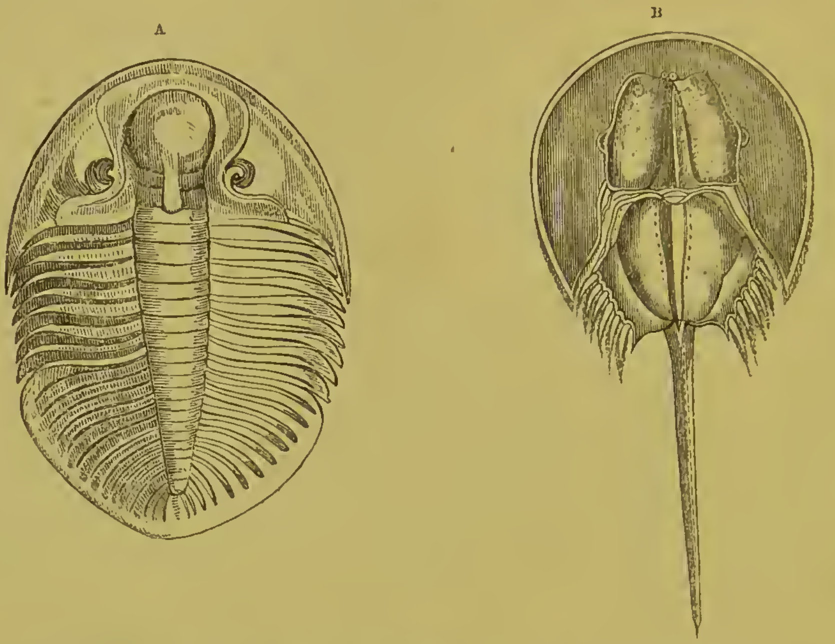
* See the "Vestiges of Creation," in which this hypothesis is put forth and sustained with great ingenuity.

gical science, however, do not seem to bear out the first of these doctrines; and the facts of Physiology lend no real support to the second. For it is easily capable of being shown, that although the doctrine of 'progressive development' as just stated *may be* true in some of its main features, —Radiata, Mollusca, and Articulata having *perhaps* existed before any Vertebrated animals left traces of their existence, Fishes having been abundant before we have any distinct evidence from the remains of Reptiles that the latter had been introduced, and Reptiles having been for a time the sole air-breathing Vertebrata, and having occupied the place (so to speak) of Birds and Mammals, when as yet these had been either very scantily produced or were altogether wanting,—yet that when we come to apply it more closely, it altogether fails. And even if the doctrine of *progressive development,* in its usual form, were true in every particular, it would afford no ground whatever for the doctrine of *transmutation,* which is not only opposed to all our experience, but which fails to account for the intimate *nexus* that so commonly unites together, not merely the higher and the lower forms of each series, but the members of different series with each other. The question how far any real support is afforded to this hypothesis by the physiological facts which have been advanced in its behalf, and which have been supposed to prove the *possibility* of such transmutation, will be more advantageously considered hereafter (CHAP. XI).

84. A more satisfactory account of the Succession of Organic Life on the surface of the globe, may probably be found in the general *plan* which has been shown to prevail in the development of the existing forms of organic structure;—namely, *the passage from the more general to the more special.* This seems to be manifested in two modes.—In the first place, we find a certain class of cases in which extinct animals, especially the earliest forms of any class that may be newly making its appearance, present indications of a closer conformity to 'archetypal generality,' than is shown in the existing animals to which they bear the closest approximation; and hence their conformity to the latter is closer in the embryo-condition of these, than in their fully developed and more specialized state. Thus the *Trilobites* (Fig. 76, A) of the Palæozoic formations are more nearly represented at the present time by the larval forms of certain Entomostracous Crustacea, than by the adult forms of any; their resemblance being peculiarly close to the larva of the *Limulus* (Fig. 76, B), which, when it quits the egg, is destitute of the peculiar bayonet-shaped weapon proceeding from the post-abdominal division of the body in the adult, and also has the cephalo-thorax relatively smaller, and the abdomen longer and more trilobed. Before the Secondary period, we have no vestiges of the higher types of Crustacean structure; the seas having been tenanted only (so far as at present known) by gigantic Entomostraca. In the secondary strata, however, we find numerous remains of the *Decapodous* order, which includes the most specialized forms of the class; but nearly all these belong to the *macrourous* section of it, which departs least from archetypal regularity. It is in the Cretaceous period, that we first meet with forms that are referrible to the intermediate *anomourous* section; and not until after the commencement of the Tertiary, do we find well-marked

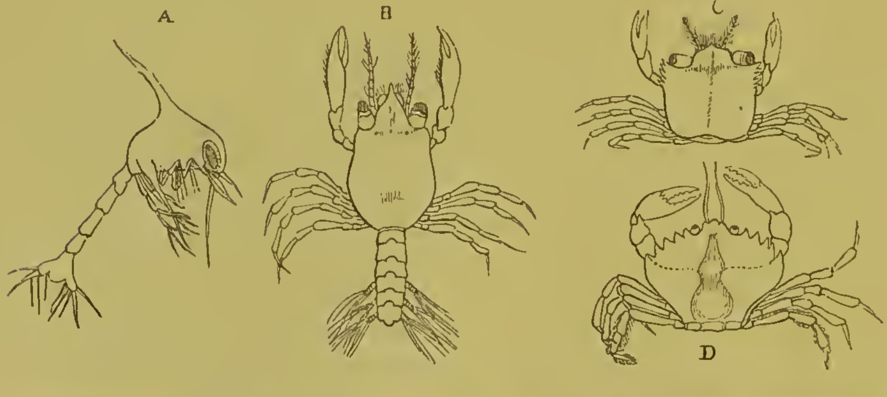
examples of the proper *brachyourous* type. Now this succession of forms is closely paralleled by that which is presented by the common Crab in the course of its development (Fig. 77); for its larva is at first essentially entomostracous, then macrourous, and then anomourous; the brachyourous form, which constitutes the greatest departure from archetype, being only assumed at the close of this series of changes.*—So again, as Prof. Owen has pointed out, since no completely ossified vertebra of a Fish has yet been discovered in the Silurian and Devonian periods, notwithstanding the

Fig. 76.



A, *Ogygia Buchii*, a Lower Silurian Trilobite: B, *Limulus moluccanus* (recent).

Fig. 77.



Metamorphosis of *Carcinus Mænas*:—A, first stage; B, second stage; C, third stage, in which it begins to assume the adult form; D, perfect form.

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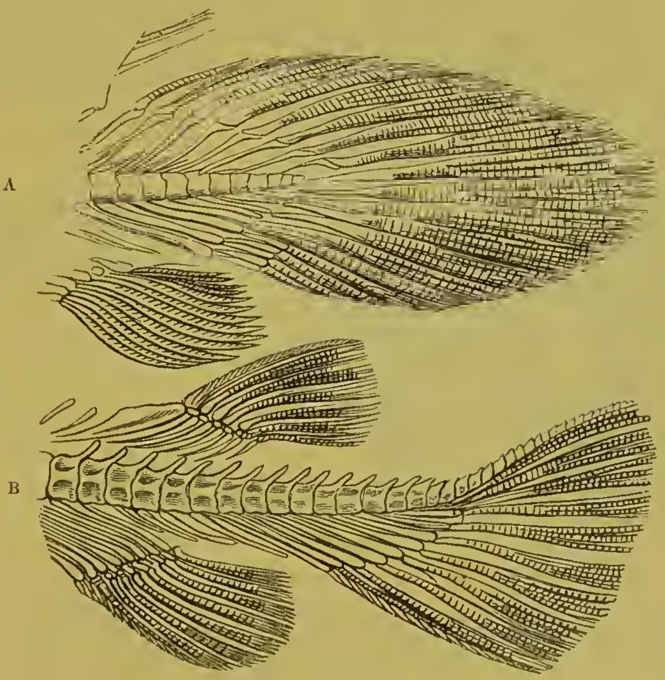
* See Prof. Owen's Hunterian Lectures "On the Generation and Development of the Invertebrated Animals," for 1849, in the "Medical Times," vol. xx., pp. 371–3.

great number of species whose remains are known to us, the evidence seems conclusive that all the Fishes of that time, whatever may have been their degree of development in other respects, could have not advanced beyond the embryonic grade of the greater number of existing Fishes, as regards the structure of their spinal column. Moreover, in nearly all the earlier Fishes, as was first pointed-out by Prof. Agassiz, we find a conformation of the tail which differs from that prevailing amongst the existing Fishes, but corresponds with that which presents itself in the embryonic state of the latter. For in most of the Osseous fishes of the present epoch, the bodies of several of the terminal caudal vertebræ coalesce, so that the spinal column appears to end abruptly, whilst their neural and hæmal arches and spines are equally developed above and below, so as to form the 'homocercal' tail represented in Fig. 78, A; in almost every Fish anterior to the Liassic period, on the other hand, the tail was formed upon the 'heterocercal' type, the vertebral column being continued onwards into its upper lobe, which is consequently the largest (B).

FIG. 78.

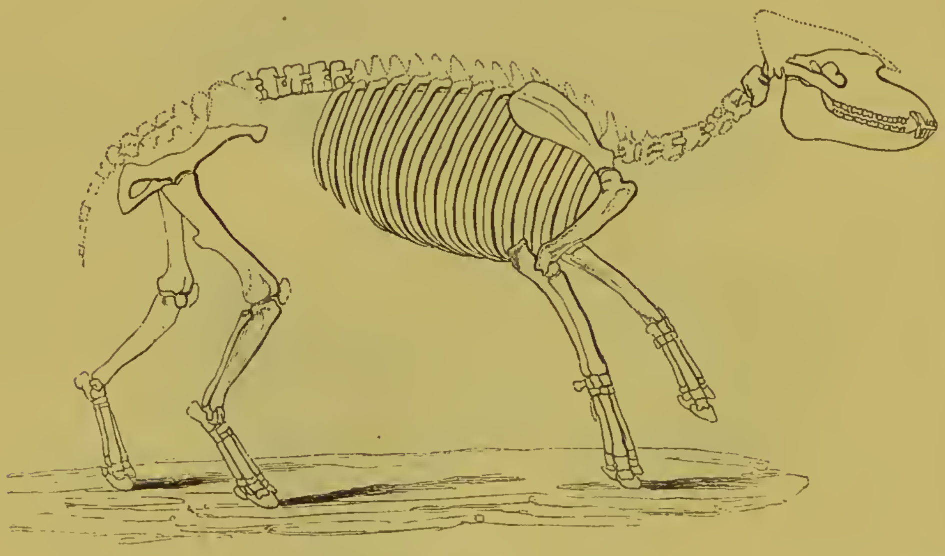


A, Homocercal tail; B, Heterocercal tail.

Now it is obiously the 'heterocercal' tail, which departs least from the 'archetype;' and we find that even those Fishes which present the 'homocercal' conformation in their mature condition, have their tails originally 'heterocercal.' Thus as the 'heterocercal' tail is the *most general* character of the class, being possessed by every fish at some period of its existence, whilst the 'homocercal' conformation is specially limited to a section of the class, the all-but-universal prevalence of the former during the earlier periods of the life of the class in our seas, and the comparatively late appearance of the latter, constitute a very remarkable example of this form of the doctrine above stated.—The Geological history of the

Reptilian class (as remarked by Prof. Owen) furnishes many illustrations of the same character. Thus in the earlier Crocodiles (as the *Teleosaurus* of the Oolitic formation), the vertebræ were biconcave, as in the embryo of the existing crocodiles; but this structure is exchanged in the succession of species, as in the development of the individual, for the ball-and-socket articulation characteristic of Reptiles generally. —So, Mammalia seem first to have become numerous, and to have presented a diversified range of forms, at the commencement of the Tertiary epoch; and in many of the earlier Mammals, a closer conformity to 'archetypal generality' is to be discovered, than in the perfected forms of their existing representatives, though paralleled (as in the previous cases) by their embryonic conditions. This is especially true in regard to the dentition; which, in most of the earlier tertiary Mammals, was remarkably conformable to the general type; the full number of 44 teeth being nearly always present, whether the animal was herbivorous or carnivorous; and the modifications whereby they were specially adapted to animal or vegetable food, being effected with far less amount of differentiation among them, than exists in the like organs at the present time. The same tendency, however, may be observed in other parts of their organization. Thus, the earliest species of *Palæotherium*, Fig. 79, (a herbivorous quadruped, having some affinity with the Tapir, but more with the Horse, of the present epoch) had the complete typical dentition, with three well-developed toes on each foot; but a later species approached the horse more closely, in the reduction of the outer and inner toes, leaving the central one much larger in proportion; and in a still later species, the outer and inner toes are much more reduced, and the form and proportions of the rest of the skeleton and teeth are brought much nearer those of the Horse, which, in the full development of only a single digit of each member, as well as in the suppression of some of the teeth and the remarkable development of others, must be considered as one of the most highly specialized forms of the order. So

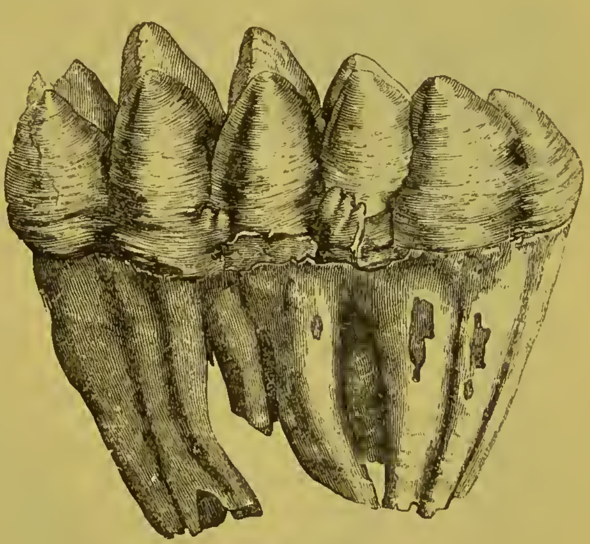
Fig. 79.



Skeleton of *Palæotherium magnum*.

in the early Mammals that most resemble the Ruminants of the present day, the most special characters of the group are wanting, or are very feebly manifested. Thus the *Dicobune, Dichodon,* and *Anoplotherium,* which may be inferred from the structure of their teeth and from the conformation of their feet to have been ruminating Mammals, were unpossessed of horns, had canines and incisors in both the upper and lower jaws, and retained through life that separation of the two metacarpal and metatarsal bones, which exists in the true Ruminants only during the embryo state, these bones subsequently coalescing in them into the single 'cannon-bone.' Hence, as Prof. Owen has remarked, they depart less widely from the archetype, than do the existing Ruminants; and are more nearly allied to the embryo-states of the latter, than to their adult forms. Again, a very wide departure from the normal type of dentition is exhibited in the Proboscidian tribe of Pachyderms, represented in the present day by the Elephant alone; for whilst the incisors of the upper jaw acquire those enormous dimensions which obtain for them the name of tusks, those of the lower are absent; and whilst the true molars not only acquire a large size, but a remarkable complexity of structure, the pre-molars are suppressed. Now the dentition of the first known representative of this order, the primeval *Mastodon,* departed far less from the typical condition, than that of the later Proboscidians; for not merely is the structure of its true molars (Fig. 80) more simple, but a permanent pre-molar is found on either side of each jaw; and in many species two incisors are developed in the lower jaw, these being sometimes retained through the whole of life. This prevalence of the normal or typical dentition among the earlier Mammals, is seen not merely in the herbivorous, but also in the carnivorous species of the older tertiary strata; thus whilst, of modern Carnivora, the Bear departs from it least, the only tooth which is wanting being the third true molar in the upper jaw, even this departure is not found in the ancient *Amphycyon,* which presents the typical formula.*

Fig. 80.



Molar tooth of *Mastodon.*

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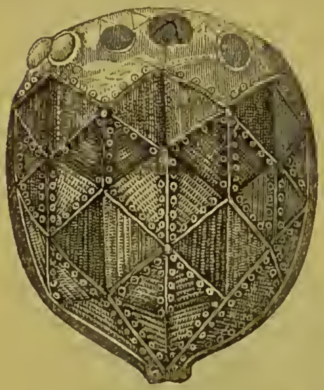
* The principle expounded in this paragraph has been prominently enunciated and illustrated by Prof. Owen in various parts of his writings. The remarkable facts here stated with respect to the dentition of Mammalia, are contained in his article 'Teeth' in the "Cyclopædia of Anatomy and Physiology," vol. iv. A masterly exposition of this general doctrine, as opposed to the 'uniformitarian' theory,—that animal and vegetable life were as highly developed in the earlier periods of geological history, as at the present time,—will be found in the "Quarterly Review," vol. lxxxix., p. 412, *et seq.*

85. But the passage from the more general to the more special is shown, not merely in the closer conformity of the more ancient forms, as compared with the existing, to archetypal generality, but also in the mode in which special characters are often first evolved. For it frequently (perhaps generally) happens, that the earliest forms of each principal group are *not the lowest;* but that they present *in combination* those characters which are found to be *separately* distributed, and *more distinctly* manifested, among groups that have subsequently made their appearance.—One of the most curious exemplifications of this principle in the *Radiated* division of the Animal kingdom, is to be found in the history of the class *Echinodermata;* for the group which seems to have attained a high development at the earliest period, is not that of *Crinoidea,* by which the class in question is most closely connected with Zoophytes, but that of *Cystidea* (Fig. 81), which (there is reason to believe) was much superior to this in general organisation. Now this order seems to have presented a most extraordinary combination of the distinctive characters of the remaining groups;* of which some appear not to have existed, and the rest to have presented a very limited range of forms, at the time when *it* was predominant. Thus, the *Crinoidea* of the Palæozoic period, though very numerous, exhibit but little variety of type; and in the complete enclosure of the body by polygonal plates, they present a closer approximation to the Cystidea, than do the Crinoidea of the Secondary period, in which the variety of forms is much greater. So, again, the *Asteriada* and *Ophiurida* of the Palæozoic period appear to have represented only a small part of the forms which those groups have since included. It is probable that the true *Echinida* did not exist at all in the Palæozoic period;† and although we are unfortunately not likely ever to obtain proof or disproof of the existence of *Holothuriada,* it cannot but be thought probable that they, too, were as yet absent. In the Secondary period, on the other hand, when the *Cystidea* had ceased to exist, we have evidence (save as to the Holothuriada, the softness of whose bodies would be likely to prevent their preservation) that they were replaced by all the orders just named; and these soon came to present a very high degree of develop-

FIG. 81.



Caryocrinites ornatus, one of the *Cystidea.*

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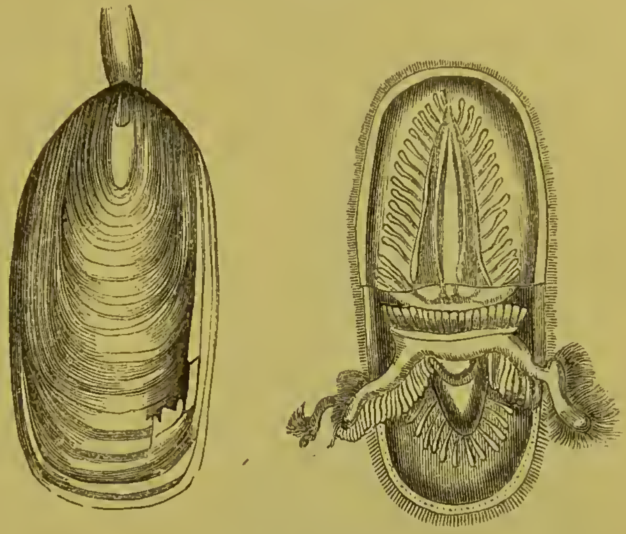
* The order *Cystidea,* as remarked by Prof. E. Forbes ("Memoirs of the Geological Survey of Great Britain," vol. ii.) seems to have been intermediate in structure between the *Crinoidea, Ophiurida, Asteriada,* and *Echinida*; for it agreed with the first in the attachment of the body by a stem, and in possessing an intestine with an anal orifice; the structure of the arms, in the species that possess them, accords with that of the second; the division of the body into lobes, in certain genera, links it with the third; and the enclosure of the body within a box-like shell, formed of polygonal plates, shows its affinity with the fourth. In addition, it may be remarked, the singleness of the generative orifice, is a strong link of connection with the *Holothuriada* (§ 40).

† The genera *Palæchinus* and *Palæocidaris,* which have been usually referred to this group, are considered by Prof. E. Forbes as connecting links between the *Cystidea* and true *Echinida,* approximating most nearly to the former.

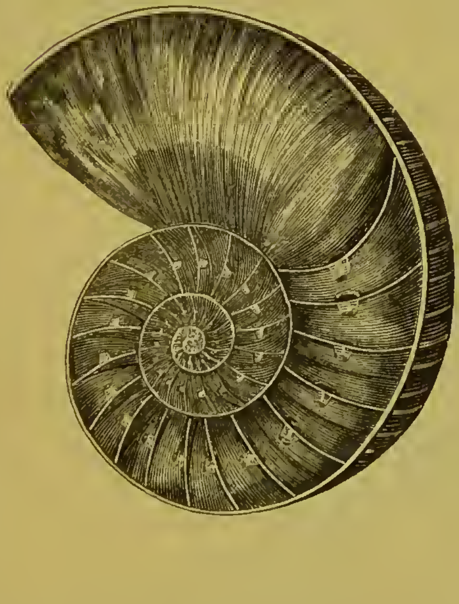
ment, dividing among them (so to speak) the characters possessed by the Cystidea, and carrying these out separately as the distinctive peculiarities of their respective types.—The earliest Bivalve Mollusk yet discovered, belongs to the existing genus *Lingula*, (Fig. 82); which, while essentially Brachiopodous in structure, has no shelly frame-work, like that of the typical Brachiopods, for the attachment of its arms, these being free throughout; whilst, on the other hand, its mantle exhibits plaited processes on its inner surface, which correspond with the early stage of formation of the specialized gills of the Lamellibranchiata; so

Fig. 82.



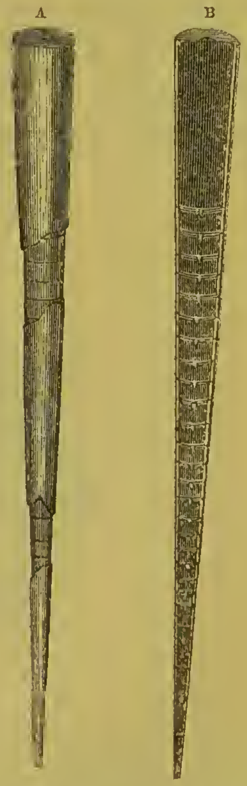
Lingula anatina.

Fig. 83.



Shell of *Nautilus pompilius*, cut open to show the chambers and the siphon.

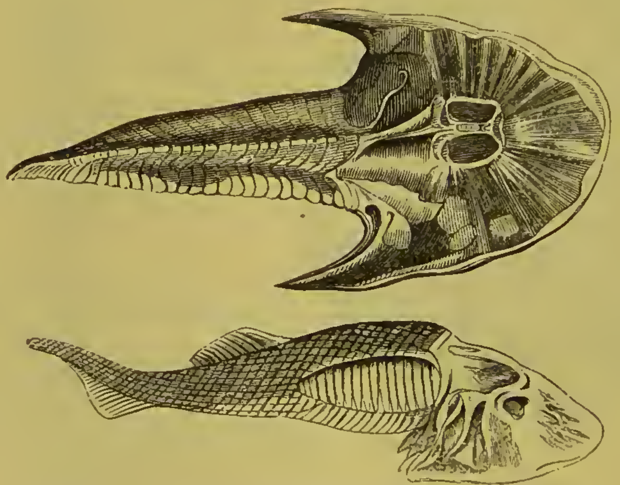
Fig. 84.



Orthoceratite. A, Exterior; B, Section, showing the chambers and siphuncle.

that, whilst more elevated, in regard to its respiratory apparatus at least, than the Brachiopods which subsequently make their appearance, it is so in virtue of its possession of Lamellibranchiate characters.—Among the higher *Mollusca,* again, we find that a prominent place in the earlier formations was occupied by the group of *Tetrabranchiata,* including the Nautilus and its allies (Figs. 83, 84); which presents the lowest development of the distinctive characters of the Cephalopod class, and which has much in common with the testaceous Gasteropods. Now there is no evidence of the existence of the *higher* order of 'Dibranchiate' Cephalopods, at that early date in the Palæozoic period at which this order had acquired an extraordinary multiplication and variety of forms; and so far it might seem that we have a progression from the lower to the higher. But the paucity of remains of typical Gasteropods, at the same period, is almost as remarkable; and some of those forms which are most abundant (*e. g.* Euomphalus and Bellerophon) present indications of close proximity to Cephalopoda. So that it would seem as if the *Nautiloid* type is really to be regarded as having occupied the place, at that period, not merely of the order above, but also (in part) of the class below; its decline and almost complete disappearance, during the Secondary epoch, being coincident with the multiplication of forms of the more typical Gasteropods, and of the higher Cephalopods.—Again, among the Fishes which were the earliest of the *Vertebrated* inhabitants of the globe, we find a remarkable assemblage of characters; some of them presenting, in the extraordinary development of the dermo-skeleton, and in the softness and probably rudimentary condition of their vertebral skeleton, an evident leaning towards the Invertebrated series; whilst others seem to have foreshadowed the class of Reptiles, an approach to which is presented, not merely by the Sharks and their allies, but by the *Sauroid* tribe of Osseous fishes, which was extremely abundant towards the end of the Palæozoic period. The *Cephalaspids* of the Devonian formation (Fig. 85) were not merely remarkable for the extraordinary development of their dermo-skeleton, which has been mistaken for that of a Trilobite, but also present,

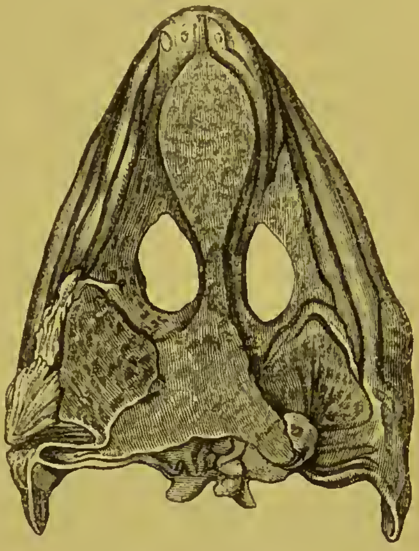
Fig. 85.



Cephalaspis Lyellii, as seen from above, and from the side.

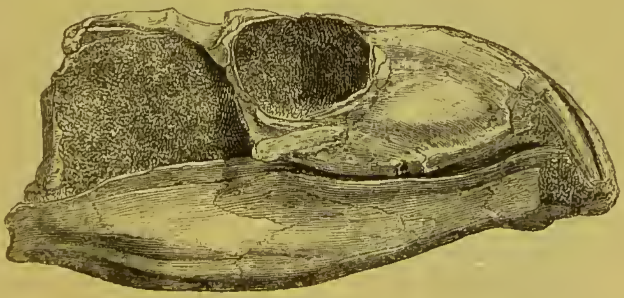
as Prof. Agassiz has pointed out, certain characters of approximation to the tadpoles of Batrachia; the breathing organs and the chief part of the alimentary apparatus having been aggregated, with the proper viscera of the cranial cavity, in an enormous cephalic enlargement, while the rest of the trunk, which dwindled to a point, seems to have been set apart for locomotion only. The Ctenoid and Cycloid orders, which (on a review of the whole class) may be undoubtedly considered as comprehending the most *typical* Fishes, did not make their appearance (so far as can be determined from the evidence of their fossil remains) until the Cretaceous period. — Turning to the air-breathing Vertebrata, again, we find that during the Secondary period, this series was chiefly represented by the class of Reptiles, which then attained its greatest importance, and included groups which represented Fishes, Birds, and Mammals respectively; thus having a more *general* character than the class at present exhibits. These groups subsequently gave place to the more *special* forms, which carry out most exclusively the Reptilian type. And when we look at the earliest forms of Reptilian life of which we have any cognizance, we find them to present very remarkable combinations of the characters which are now distributed among different groups. Thus, the *Labyrinthodon* (Fig. 86) of the Triassic formation, appears to have been essentially *Batrachian* in its structure, but to have possessed some characters of the *Crocodilian* order.

FIG. 86.



Skull of *Labyrinthodon*.

FIG. 87.

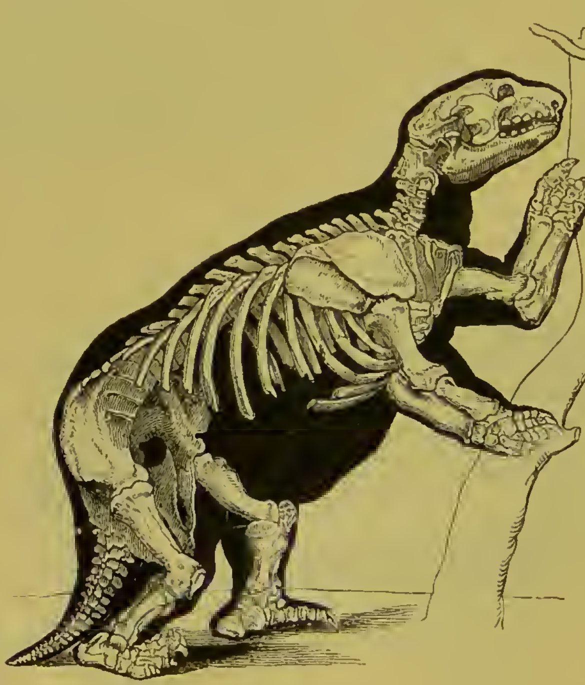


Skull of *Rhyncosaurus*.

The same formation contains remains of the *Rhyncosaurus* (Fig. 87), which, while essentially *Saurian* in its general structure, had the horny mandibles, and probably many other characters, of the *Chelonia*. From the same or a somewhat anterior epoch, we have the remains of the

Dicynodon; which seems, along with Chelonian, Crocodilian, and Saurian characters, to have possessed the peculiarly Mammalian feature of a pair of tusks growing from persistent pulps. So, again, the *Ichthyosaurus,* whilst essentially Saurian in its osteology, had not merely the bi-concave vertebræ of a Fish, but paddles of a Cetacean type, and a peculiar sterno-acromial apparatus resembling that of the Ornithorhyncus. And the *Plesiosaurus,* which is spoken-of by Cuvier as the most 'heteroclite' of all the fossil animals known to him, possessed the teeth of the Crocodile with the head of a Lizard, a neck that resembled the body of a Serpent, the ribs of a Chameleon, and paddles still more decidedly Cetacean.—In the early history of the class Mammalia, so far as known to us, the same general plan may be traced. The only order that is distinctly recognizable by the remains preserved in the Secondary strata, is that of *Marsupialia,* which has much in common with the Oviparous Vertebrata. Near the commencement of the Tertiary epoch, remains of *Pachydermata* are abundant; but these were for the most part different from those of the present epoch, containing combinations of characters which are now distributed among several distinct families, and presenting also a closer approximation to the Herbivorous Cetaceans on the one hand, and to the Ruminants on the other, than is exhibited by any existing species of the order. A most curious combination of characters is presented by the extinct *Toxodon;* which had the incisors of Rodentia, many of the cranial characters of Cetacea, the molar teeth and massive stature of the Gravigrade Edentata, with a general conformation which seems referable to the Pachyderm type. The Gravigrade Edentata, of which the *Mylodon* (Fig. 88) is a characteristic example, themselves afford a most interesting

Fig. 88.



Skeleton of *Mylodon.*

illustration of this general principle; for whilst essentially allied to the modern Sloths in their general structure, they had not only affinities to other sub-divisions of the Edentate order, but also presented links of transition to the massive Pachyderms. This group is now entirely extinct.*

86. In regard to the Geological history of the Vegetable kingdom, it must be admitted that our knowledge is still very imperfect; in consequence of the small number of cases in which the internal structure and fructification of the earlier plants have been preserved, in a condition that allows of the exact determination of their characters and affinities. So far as our present information extends, however, it is fully in harmony with the above doctrine; the characteristic Flora of the Coal-formation appearing to have been chiefly composed of *Coniferæ*, which constitute a connecting link between the Phanerogamia and Cryptogamia; and of these Coniferæ, while some may have been nearly allied to existing forms, the great majority (*Sigillariæ*, *Lepidodendra*, *Calamites*, &c.) appear to have presented such a combination of the characters of the Coniferæ with those of the higher Cryptogamia, as no existing group exhibits.

87. So far as at present known, therefore, the general facts of Palæontology appear to sanction the belief, that *the same plan* may be traced out in what may be called *the general life of the globe*, as in the *individual life* of every one of the forms of organised being which now people it; and that in the successive introduction of the several groups composing the Animal and Vegetable kingdoms respectively, the progression was not so much from the lower to the higher forms, as from the more general to the more special,—from those which were in closest relationship to each other, to those that are most isolated as types of their respective groups. And thus it has happened, that, as every Palæontologist must be ready to admit, a large proportion of the extinct forms of Animals and Vegetables must rank, in any philosophical system of classification, as *osculant* or *transitional* forms; connecting together the groups which seem naturally to assemble round existing types, and seldom standing as centres round which existing forms should be arranged.—It would be premature and presumptuous to assert that such *was* the plan, on which the progressive evolution of the great scheme of Organic Creation has proceeded; but the foregoing indications may be thought sufficient to justify the assertion, that such *may have* been the plan. If this view have a foundation in truth, the development of the principle in all its completeness must be left for the time, when Palæontology shall possess, as the result of the accumulated labours of many generations (it may be) of industrious explorers, a collection of information respecting the *past* distribution of Animal and Vegetable life upon our globe, in some degree comparable to that to which the Natural History of the present time is rapidly attaining.†

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* It has been by the researches of Prof. Owen, more than by those of any other Comparative Anatomist of modern times, that the curious order of facts above referred-to,—in regard to Vertebrata at least,—has been brought to light.

† In the foregoing chapter, the Author has endeavoured to set forth, with the additional illustrations afforded by later Anatomical and Embryological researches, the views first propounded by Von Baer, in his masterly work, "Uber Entwickelungs-Geschichte der Thiere," 1828, and recently made more accessible to English readers by Mr. Huxley's translation, in "Taylor's Scientific Memoirs," 1852-3.

CHAPTER II.

GENERAL VIEW OF THE VITAL OPERATIONS OF LIVING BEINGS, AND OF THEIR MUTUAL RELATIONS.

88. The study of the various forms and combinations of Organic Structure, which present themselves to the Anatomist in his general survey of the Animated Creation, and the determination of the plan according to which we may suppose them to have been evolved, constitute a department of Biological enquiry that is quite distinct from that on which we are now to enter,—namely, the study of the *changes which take place in these bodies*, during their existence as *living organisms:* —a connecting link between the two being furnished by the phenomena of *Development*, which strictly belong to the last-mentioned category, although, as we have seen, they afford most essential assistance in the preceding enquiry. As it should be the principal aim of the scientific Physiologist, to determine the laws according to which these changes take place, it is his first business to collect and compare all the facts of the same character, which he can draw from the most extended observation of the phenomena of Life. The changes which occur during the life of *any one* being, are of themselves inadequate to furnish the required information: since this presents us only with a group of dissimilar phenomena, incapable of comparison with each other, or permitting it but to a low degree. Were we, for example, to derive all our notions of Physiology from the history of one of the simple Cellular Plants, we should obtain but very vague ideas as to the character of its different nutritive processes; since we cannot separate these from one another, so as to be enabled to investigate them apart. And, on the other hand, we should be apt to form very erroneous conceptions of the essential conditions of these processes, were we to study them only in that specialized condition which they present in the most complete Animal, and were to reason thence as to their dependence upon particular kinds of structure. It is only, then, from a comprehensive survey of the whole Organised Creation, —embracing the unobtrusive manifestations of vitality which Nature presents at one extremity of the scale (as if to show the real simplicity of her operations), as well as those obvious changes which she every moment displays to us in her most elaborate and varied works (as if to display the endless fertility of her resources),—that any laws possessing a claim to generality can be deduced.

89. In every living Organism of a complex nature, we can readily distinguish a great variety of actions, resulting from the exercise of the different powers of its several component parts; and these actions are said to be the *functions* of the structures by whose instrumentality they are performed. Thus it is the 'function' of a Muscle, to contract on the application of a stimulus; and that of a Nerve, to receive and to convey sensory or motor impressions. When we look at such an organism,

however, *as a whole*, we perceive that these changes may be associated into groups, in accordance with their relations to each other; each group consisting of an assemblage of actions, which, though differing among themselves, concur in effecting some determinate and important purpose. To these groups of actions, also, the name of *Functions* is applied, but not in the same sense as before. Thus when we speak of the 'Function of Respiration,' we imply the assemblage of those separate actions which concur in effecting the aeration of the nutritious fluid, by exposing it to the atmosphere, or to the gases diffused through water, so as to effect a certain change in its composition. Simple as this operation appears, many provisions are required in the higher organisms for its effectual performance. In the first place, there must be an aerating surface, consisting of a thin membrane permeable to gases; on one side of which the blood may be spread out, while the air is in contact with the other. Secondly, there must be a provision for continually renewing the nutritious fluid which is brought to this surface, in order that the whole mass of it may be equally benefited by the process. And thirdly, the stratum of air must also be renewed, as frequently as its constituents have undergone any essential change. In each of these subdivisions, a great many diverse actions are involved; yet all of them are included under the same general term, since they concur to the same fundamental purpose.—Now if we analyse that series of phenomena, which constitute the 'Function of Respiration' in one of those higher Animals (Man, for example) in which it presents its greatest complexity, we shall find that whilst some of them are indispensable to the continuance of life, and can only be performed under the conditions supplied by the organised system, others are merely superadded for the purpose of facilitating these; and the latter, if from any cause not performed by the mechanism contrived for their production, may be artificially imitated, with a degree of success exactly proportional to the completeness of the imitation. The essential part of that function being the aeration of the blood, all the other changes which are associated together as partaking in it must be regarded as non-essential, sharing in it only by contributing to this—the real constituent of it. Thus the alterations in the capacity of the chest, which are effected by the actions of the diaphragm, and have for their object the renewal of the quantity of air in contact with the aerating surface, are really a part of the functions of the Muscular and Nervous systems; and are only associated under that of Respiration, on account of their obvious tendency towards its essential purpose. They have no share in the production of the aeration of the blood, except by supplying its conditions; and if these conditions can be supplied independently of them, the essential part of the function will be performed as when they were concerned in it.*

90. By an analysis of this kind applied to the other Functions, similar

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* Thus in *Asphyxia*, the deficient supply of arterialised blood to the brain soon paralyses its functions; and the nervous stimulus required for the respiratory movements being withheld, those movements cease. But, if the chest be artificially inflated, and emptied again by pressure, and these alternate movements be sufficiently prolonged to re-excite the circulation of the blood through the lungs, by aerating that which had been stagnated there, the whole train of vital actions may be again set in motion. Or, if the cessation of the respiratory movements result from a cause primarily affecting the nervous system—as when narcotism

conclusions might be arrived-at respecting their essential character; for it will appear in every one of them, that some of the changes which are thus grouped together are *essential*, whilst others are *superadded*. But these conclusions do not possess the same certainty as if they were founded upon a broader basis; nor are they so easily attained. For, to revert to the instance just quoted, *observation* alone of the vital phenomena of the lower animals, will reveal what could only be determined in the higher by *experiment*. Until an experiment (the insufflation of the chest) had been found successful in continuing the aeration of the blood, it could not be certainly known that the respiratory movements had not some further share in the function, than that of mechanically renewing the air in apposition with the circulating fluid. But when the conditions of the function are examined in the lower animals, it is found that these are varied (the essential part being everywhere the same) to suit the respective circumstances of their existence. Thus, many Reptiles, having no diaphragm, are obliged to fill the lungs with air by a process which resembles swallowing. In Fishes and other aquatic animals, to have introduced the necessary amount of the dense element they inhabit into the interior of the system, would have occasioned an immense expenditure of muscular power; and the required purpose is answered, by sending the blood to meet the water which is in apposition with the external surface. And in those simple creatures, in which the fluids appear equally diffused through the whole system, their required aeration is effected by the mere contact of the water with the general surface; the stratum in immediate apposition with it being renewed, either by their own change of place, or, if they are fixed to a particular spot, through the means they possess of creating currents, by which their supply of food also is brought to them. And, going still further, we find the essential part of the function of Respiration performed in Plants without any movement whatever; the wide extension of the surface in contact with the atmosphere, affording all the requisite facility for the aeration of the circulating fluid.—It is by such a mode of analysis, then, that we are most certainly enabled to distinguish the essential conditions of vital phenomena, from those which are superadded or accidental; and it is this which will form the subject of the greater part of the present Treatise.

91. When we examine and compare the several Functions, or assemblages of Vital Actions grouped together according to the principle just set forth, we find that they are themselves capable of some degree of classification. Indeed the distinction between the groups into which they may be arranged, is one of fundamental importance in Physiology. If we contemplate the history of the life of a Plant, we perceive that it grows from a minute germ to a fabric of sometimes gigantic size, generates a large quantity of organic compounds which it appropriates as the materials of its own structure, and multiplies its species by the production of germs similar to that from which it originated; but that it performs all these complex operations, without (so far as we can perceive) either feeling or thinking, without consciousness or the exertion of will. All its vital

is induced by poisoning with opium—and the blood be, in consequence, stagnated in the lungs by the want of aeration, this change, so essential to the continuance of vitality, may be prolonged by artificial respiration, until the narcotism subsides.

operations, therefore, are grouped together under the general designation of Functions of *Organic* or *Vegetative* life; and they are subdivided into those concerned in the maintenance and extension of the structure of the *individual*, which are termed functions of *Nutrition;* and those to which the perpetuation of the *species*, by the *Generation* of a succession of individuals, is due.—The great feature of the Nutritive operations in the Plant, is their *constructive* character. They seem as if destined merely for the building-up and extension of the fabric; and to this extension there appears to be in some cases no determinate limit. It is important to remark, however, that the growth of the more *permanent* parts of the fabric is only provided-for by the successive development, decay, and renewal of parts whose existence is *temporary;* the growth of the dense, durable, but almost inert woody structure, being dependent upon the continual production of new leaves, composed of a soft, transitory, but active cellular parenchyma.—Sooner or later, however, the life of the individual must come to an end; and the race itself must become extinct, were it not for the special provision which is made for its continuance, in the Generative function. This consists in the evolution of germs, which, becoming detached from the parent, are able to support an independent existence, usually at the expense, however, in the first instance, of nutriment in some way provided by the being that gave them origin; they gradually become developed into its likeness, perform all the vital operations characteristic of it, and in their turn originate a new generation by a similar process.

92. Now, it may be observed, before proceeding further, that there is a certain degree of antagonism between the Nutritive and the Generative functions, the one set being executed at the expense of the other. The generative apparatus derives the materials of its operations through the nutritive system, and is entirely dependent upon it for the continuance of its activity. If, therefore, the generative activity be excessive, it will necessarily draw-off from the fabric at large some portion of the aliment destined for *its* maintenance. It may be universally observed that, where the nutritive functions are particularly active in supporting the *individual*, the reproductive system is in a corresponding degree undeveloped,—and *vice versâ.* Thus, in the Algæ, the dimensions attained by single plants exceed those exhibited by any other organised being; and in this class the fructifying system is often obscure, and sometimes even undiscoverable. In the Fungi, on the other hand, almost the whole plant seems made up of reproductive organs; and as soon as these have brought their germs to maturity, it ceases to exist. In the Flowering-Plant, moreover, it is well known that an over-supply of nutriment will cause an evolution of leaves at the expense of the flowers, so that what actually would have been flower-buds, are converted into leaf-buds; or the parts of the flower essentially concerned in reproduction, namely, the stamens and pistil, are converted into foliaceous expansions, as in the production of 'double' flowers from 'single' ones by cultivation; or the fertile florets of the 'disk' in composite species, such as the Dahlia, are converted into the barren but expanded florets of the 'ray.' And the gardener who wishes to render a tree more productive of fruit, is obliged to restrain its luxuriance by pruning, or to limit its supply of food by trenching round the roots.—The same antagonism may be witnessed in

the Animal Kingdom; but as a third element (the sensori-motor apparatus) here comes into operation, it is not always so apparent. It appears to be a universal principle, however, that during the period of rapid growth, when all the energies of the system are concentrated upon the perfection of its individual structure, the reproductive system remains dormant, and is not aroused until the diminished activity of the nutritive functions allows it to be exercised without injury to them. Thus, in the Larva condition of the Insect, the assimilation of food and the increase of its bulk seem the sole objects of its existence; its locomotive powers are only adapted to obtain nourishment that is within easy reach, to which it is directed by the position of its egg, and by an unerring instinct that seems to have no other end. The same is the case, more or less, with all young animals; although there are few in which voracity is so predominant a characteristic. In the Imago, or perfect Insect, on the other hand, the fulfilment of the purposes of its generative system appears to be the chief and often the only end of its being. The increased locomotive powers which are conferred upon it, are evidently designed to enable it to seek its mate; its instinct appears to direct it to this object, as before to the acquisition of food; it now shuns the aliment it previously devoured with avidity, and frequently dies as soon as the foundation is laid for a new generation, without having taken any nutriment from the period of its first metamorphosis. In the adult condition of the higher Animals, again, it is always found that, as in Plants, an excessive activity of the nutritive functions indisposes the system to the performance of the reproductive; a moderately-fed population multiplying (cæteris paribus) more rapidly than one habituated to a plethoric condition.

93. On analysing the operations which take place in the Animal body, we find that a large number of them are of essentially the same character with the foregoing, and differ only in the conditions under which they are performed; so that we may, in fact, readily separate the *Organic* functions, which are directly concerned in the development and maintenance of the fabric, from the *Animal* functions, which render the individual conscious of external impressions, and capable of executing spontaneous movements. The relative development of the organs destined to these two purposes, differs considerably in the several groups of Animals, as we have already in part seen (CHAP. I.) The life of a Zoophyte is upon the whole much more 'vegetative' than 'animal'; and we perceive in it, not merely the very feeble development of those powers which are peculiar to the Animal kingdom, but also that tendency to indefinite extension which is characteristic of the Plant. In the perfect Insect, we have the opposite extreme; the most active powers of motion, and sensations of which some (at least) are very acute, being combined with a low development of the organs of nutrition. In Man and his allies, we have less active powers of locomotion, but a much greater variety of Animal faculties; whilst the instruments of the organic or nutritive operations attain their highest development, and their greatest degree of mutual dependence. We see in the fabric of all beings in which the Animal powers are much developed, an almost entire want of that tendency to indefinite extension which is so characteristic of the Plant; and when the large amount of food consumed by them is considered, the question naturally

arises, to what purpose this food is applied, and what is the necessity for the continued activity of the Organic functions, when once the fabric has attained the limit of its development.—The answer to this question lies in the fact, that the exercise of the Animal functions is essentially *destructive* of their instruments; every operation of the Nervous and Muscular systems requiring, as its necessary condition, a disintegration of a certain part of their tissues, probably by their elements being caused to unite with oxygen. The duration of the existence of those tissues varies inversely to the use that is made of them; being less, as their functional activity is greater. Hence, when an Animal is very inactive, it requires but little nutrition; if it be in moderate activity, there is a moderate demand for food; but if its Nervous and Muscular energy be frequently and powerfully aroused, the supply must be increased, in order to maintain the vigour of its system. In like manner, the amount of certain products of excretion, which result from the disintegration of the Nervous and Muscular tissues, increases with their activity, and diminishes in proportion to their freedom from exertion. (See CHAP. IX.)

94. In the Animal fabric, then, among the higher classes at least, the function or purpose of the organs of Vegetative life is not so much the extension of the fabric,—for this has certain definite limits,—as the maintenance of its integrity, by the reparation of the destructive effects of the exercise of the purely Animal powers. Thus, by the operations of Digestion, Assimilation, and Circulation, the nutritious materials are prepared and conveyed to the points where they are required; the Circulation of blood also serves to distribute oxygen, which is introduced by the Respiratory process; and it has further for its office, to convey away the products of that decomposition of the Muscular and Nervous tissues, which results from their functional activity,—these products being destined to be separated by the Respiratory and other Excreting operations. In the performance of the Organic functions of Animals, as in those of Plants, there is a continual new production, decay, exuviation, and renewal, of the cells by whose instrumentality they are effected; which altogether effect a change not less complete than that of the leaves in Plants. But it takes place within the penetralia of the system, in such a manner as to elude observation, except that of the most scrutinizing kind; and it has been in bringing this into view, that the Microscope has rendered one of its most essential services in Physiology.

95. The regular maintenance of the functions of Animal life is thus entirely dependent upon the due performance of the Nutritive operations. But there also exists a connection between the Organic and Animal functions, of an entirely reverse kind; for the conditions of Animal existence render the former in a great degree dependent on the latter. In the acquisition of food, for example, the Animal has to make use of its senses, its psychical faculties, and its power of locomotion, to procure that which the Plant, from the different provision made for its support, can obtain without any such assistance. Moreover, the propulsion of the food along the alimentary canal of the former, requires a series of operations, in which the Nervous and Muscular systems are together involved at the two extremes (simple muscular contractility being alone employed through the greater part of the intestinal canal); and thus we see that the change in the conditions required for the ingestion of food by

Animals, has rendered necessary the introduction of additional elements into the apparatus, to which nothing comparable was to be found in Plants. The same may be observed, as already pointed out, in the operations of the Respiratory apparatus. And it may be stated as a general rule, that the more exalted is the *animality* of any particular being (or, in other words, the more complete the manifestation of characters peculiarly animal), the more closely are the organic functions brought into relation with it.*

96. From what has been said, then, it appears that all the functions of the body, among the higher Animals, are so completely bound up together, that none can be suspended without the cessation of the rest. The properties of all the tissues and organs are dependent upon their regular Nutrition by a due supply of perfectly-elaborated blood; and this cannot be effected, unless the functions of Circulation, Respiration, and Secretion, be performed with regularity,—the first being necessary to convey the supply of nutritious fluid, and the two latter to eliminate from it the impurities with which it is continually becoming charged. The Respiration cannot be maintained, without the integrity of a certain part of the nervous system: and the due action of this, again, is dependent upon its regular nutrition. The materials necessary for the replacement of such as are continually being separated from the blood, can only be supplied by the Absorption of ingested aliment; and this cannot be accomplished, without the preliminary process of Digestion. The Ingestion of food into the stomach, again, is dependent, like the actions of respiration, upon the operations of a certain part of the muscular apparatus and of the nervous centres; and the previous acquirement of food necessarily involves the purely Animal powers. On the other hand, the functions of Animal life are even more closely dependent upon their proper *pabulum*, than are those of Nutrition in general: for many tissues will retain their several properties, and even their power of growth and extension, for a much longer period after a general interruption of the circulation, than will the Nervous structure; the action of which is instantaneously affected by a cessation of the due supply of blood, or by a depravation of its quality.

97. Yet, however intimate may be the bond of union between the Organic and Animal functions, the former are never *immediately* dependent upon the latter; although, as already shown, they generally depend upon them for the conditions of their maintenance. There is no good reason to believe that 'nervous agency' is *essential* to the processes of Nutrition and Secretion in Animals, any more than to the corresponding processes in Plants. This is a question which may be more certainly determined by *observation*, than by any possible *experiment*. That these processes are very readily *influenced by* changes in the condition of

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* A simple illustration will render this evident.—In certain of the lower tribes of animals, whose locomotive powers are feeble and general habits inactive, the circulation of nutritive fluid is carried on nearly in the same manner as in plants; there is no central organ for propelling it through the vessels, and ensuring its regular and equable distribution; and its motion appears dependent upon the forces created in the individual parts themselves. In the higher classes, on the other hand, the comparative activity of all the functions, and the peculiar dependence of those of animal life upon a constant supply of the vital fluid, require a much more elaborate apparatus, and especially a central power, by which the movements of that fluid through the individual parts may be harmonised, directed, and controlled.

the nervous system, is universally admitted; and it is the intimacy of this connection, which has given rise to the idea of a relation of *dependence*, and which prevents that idea from being experimentally disproved. In order to cut off *all* nervous communication from any portion of the organism—a gland for example,—so violent an operation is required (involving no less than the complete division of the blood-vessels, on which a plexus of ganglionic nerves is minutely distributed), that it is impossible to say that the disturbance of the function may not be owing to the shock produced on the general system. Observation shows us, however, that these processes are performed in the most complex and elaborate manner by Vegetables, in which all the attempts that have been made to prove the existence of a nervous system have signally failed (these attempts seeming to have been only excited by an indisposition to admit the possibility of any vital actions being independent of 'nervous influence');—that the lowest Animals appear equally destitute of a nervous apparatus destined to influence them;—that in the higher classes, there are many tissues into which nerves cannot be traced, and which yet exhibit as much vital activity as those which are in most intimate relation with nerves;—and that in their early embryonic condition, the formative operations are performed with their greatest energy, at a period when it is quite certain that no nerves have yet been developed.

98. Still, there can be little doubt that a most intimate connection is established, in the higher animals, between organic processes essentially independent of each other, by the instrumentality of the Nervous system, and especially by that part of it known as the 'Sympathetic;' and this seems to have relation to the necessity which arises, from the complication and specialisation of the Organic functions, for their being harmonised and kept in sympathy with each other, and with the conditions of the Animal system, by some mode of communication more certain and direct than that afforded by the circulating apparatus, which is their only bond of union in Plants. For it must be remembered that it is in the very nature of high development, that the differentiation of function, whereby mutually-connected operations are assigned to separate organs, should be accompanied by a far closer interdependence of these operations, than exists between the actions of an organism whose several parts are little else than repetitions of each other. And there is no real difficulty in admitting, that nerve-force may have a relation no less definite to acts of nutrition, than it has to mental changes or to acts of muscular contraction; for, just as an electric current, set in motion by certain chemical reactions, is capable of influencing the chemical reaction of substances submitted to its agency, so may it be fairly anticipated that nervous power, itself the result of a certain class of nutritive operations (of which it may be considered the highest product), should be able to modify the course of those operations elsewhere. (See GENERAL PHYSIOLOGY.)

99. The *Absorption* of alimentary materials, which is the first in the train of strictly Vital operations, is common to Plants and to Animals, although performed under somewhat different conditions in the two Kingdoms. The *Plant* derives its support immediately from the surrounding elements; it is fixed in the spot where its germ was cast; and it neither possesses a will to move in search of food, nor any locomotive organs for

so doing. By the peculiar endowments of its roots, however, it becomes possessed of a certain power of obtaining aliment not immediately within its reach (§ 175). The *Animal* usually has a recipient cavity, in which its food, consisting of organic compounds previously formed, undergoes a certain preliminary preparation or *Digestion.* The introduction of food into this cavity, or its *ingestion,* seems more and more dependent upon the animal functions, in proportion as we ascend the scale. The ciliary movements of the lower classes of animals, which produce rapid currents in the water that surrounds them, and thus bring a supply of food to the entrance of the digestive cavity, can scarcely be regarded as having any other than the automatic character which we know them to possess in the higher. In animals of more complex structure, the process of obtaining food requires a much greater variety of movements, which are executed by the instrumentality of the Muscular and Nervous systems; but these may still be regarded as not involving changes of a psychical character. Rising still higher, however, we find the Psychical endowments of the animal evidently concerned in procuring the means of its support; and in Man, in whom these exist in their highest perfection, the reliance upon them is necessarily the greatest, his bodily organisation not being adapted for the supply of his physical wants, except under the direction of his Intelligence.—The products of the Digestive operation may pass by simple transudation from the digestive sac into the cavity that usually surrounds it; or they may be taken-up by vessels distributed on its walls. In the higher Animals, we find that this absorption is not effected by the blood-vessels alone, but that it is partly performed by a special set of *Lacteal Absorbents* spread over the walls of the digestive cavity; these discharge the matters they have taken-up, into the current of the circulation; and it is probable that in this 'absorbent system' that function of Assimilation commences, by which the crude material is prepared for taking part in the formative processes. There is another division of this 'absorbent system,' which extends itself through the body, and which seems destined to collect the superfluous nutritive material that may have escaped from the blood-vessels, together (perhaps) with such as may have served its purpose in the system, and have died without decomposing, so as to be again available as an alimentary substance; and this *Lymphatic* system of vessels, also, would seem to partake in the Assimilative operation, of which we have presently to speak.

100. The alimentary materials taken up by the absorbent process, are carried by the *Circulation* into all parts of the fabric. This movement, so important in the highest classes of Plants and Animals, becomes less necessary in the lower, where the absorbent surface is in more immediate relation with the parts to be supplied with nourishment. Besides affording a continued supply of nutrient material for the maintenance of the formative operations, the circulating system of Animals is usually the means of conveying to their nervo-muscular apparatus the oxygen whose presence is a necessary condition of its vital activity. It also serves to take up the effete matters which are set free by the 'waste' of the system, and to convey these to the organs provided for their elimination. The Circulation in Animals, as in Plants, is entirely independent of the will, cannot be in the least degree controlled by it, and, in its usual condition, is even unaccompanied with consciousness. The Muscular apparatus

is concerned in it, only to give to it the energy and regularity which the conditions of animal existence require (§ 95 *note*); and Nervous agency merely brings it into sympathy with other operations of the corporeal and mental systems.

101. The alimentary materials first taken up by the absorbent process, must undergo various changes by *Assimilation*, before they can be introduced into the composition of the organised fabric. There is much difficulty, however, in tracing these with precision, either in the Animal or in the Vegetable economy. The first step which is perceptible in the latter, is the formation of *organic compounds* by a new combination of the elements supplied by the food, which appears to commence as soon as these elements are absorbed. In the former, these organic compounds are directly supplied by the food; and this preliminary operation is consequently not required. From whichever source they are derived, however, these organic compounds appear to be subjected, whilst yet circulating in the liquid form, to a vital influence, exerted either by the living tissues through which they flow, or by cells that are floating in the stream, or perhaps by both; for we find them, without any detectable change in ultimate composition, exhibiting peculiar properties, which mark the transition from the crude form in which they are received into the body, towards the condition of living tissue. The 'protoplasma' of the Plant, and the 'liquor sanguinis' of the Animal, are very different from mere admixtures of gum, albumen, water, and other organic compounds, but show a capacity for becoming organised, which these do not possess; hence their peculiar ingredients are designated as *organisable* or *plastic* substances. From these materials, the individual tissues of the fabric are developed and renewed by the process of *Nutrition;* the elements of each tissue deriving from the plastic fluid that portion which their composition may require. This process is influenced in the Animal, through the Nervous system, by conditions of the mind or of the general fabric; but it does not seem to be *maintained* by any such influence (§ 98). It is of course dependent, however, upon the continued supply of blood, and cannot long continue if the Circulation be brought to a stand; still there is evidence that it may go on for a time, at the expense of the blood contained in the vessels of a part, after the current has ceased to flow.

102. In order to preserve the circulating fluid in the state required for the due performance of its important functions, means are provided for separating and carrying out of the system whatever may be superfluous or injurious in its constituent parts; as well as for elaborating from it certain fluids having their destined use in the economy. These changes may be comprehended in the general term *Secretion*, the former constituting the special function of *Excretion.* This is one no less important to the welfare of the system, than is the absorption of new aliment; and in proportion to the complexity of the structure, and to the diversity of its actions, do we find a multiplication of the excreting organs, as well as a variety in their products. The elimination of superfluous water by *Exhalation*, and of carbonic acid by *Respiration*, are constant, however, in all living beings; and in Animals we find an excretion of a highly azotized compound to be nearly as universal. These changes seem to have no more immediate dependence upon the Nervous system, than have those of nutrition; and they will take place, to a certain extent, after the

final extinction of the animal powers. Wherever a proper Circulation exists, however, they are most intimately dependent upon its maintenance, and soon come to an end if it ceases; but it is probable that, in particular cases, they are kept up by the *capillary* circulation, when the general propulsive force is no longer acting.

103. The function of Nutrition is exercised, not merely in renovating and extending the single fabric which first originates in the germ, but also, throughout the Vegetable kingdom, as well as in a large proportion of the Animal, in developing parts which can maintain an independent existence, and which are commonly accounted distinct 'individuals.' Thus, in the Protophyta and the Protozoa, each new cell formed by the *subdivision* of those previously existing, may be regarded either as a part of the parent structure, or as a distinct individual, being capable of living, growing, and multiplying by itself. Even in higher members of both kingdoms, a like Multiplication of (so-called) individuals is effected by the development of *gemmæ;* a process which corresponds in every essential particular with that of ordinary Nutrition, and which is no more dependent than *it* is upon the activity of the Animal functions. And in many Animals, in which this power does not extend to the multiplication of parts capable of maintaining an independent existence, it suffices to reproduce entire organs which have been removed, or (sometimes) to multiply them beyond their regular number.

104. The true *Generative* function, by which the foundation of an entirely new organism is laid, is essentially antagonistic (as already remarked) to the preceding; for instead of consisting in the extension of the original fabric by the subdivision of its cells, or by the formation of new tissue in connection with the old, it requires, as its essential condition, the *reunion* of the contents of two cells, which, though not differentiated in the lowest Plants and Animals, either from those of the remainder of the organism, or from each other, are distinguishable in all but these as 'sperm-cells' and 'germ-cells.' The concurrent action of these takes place in Plants without any interference of will, or excitement of consciousness, on the part of the individual; the two organs being sometimes united in the same being (as in hermaphrodite flowers), or, if separated (as in monœcious species), being brought into the required relation by external assistance, as when the pollen of one flower is conveyed to the stigma of another at some distance, by the agency of the wind, of insects, &c. There are some Animals in which the two sets of organs are united in the same individual; and the actions necessary to bring them into relation seem no more to depend upon conscious agency, than do those which are concerned in the aeration of the blood. But in the higher classes, where the organs exist in separate individuals, the nervo-muscular apparatus excited by powerful sensations is evidently the instrument by which they are brought into relation with one another; and in Man, where the sensations are connected with a nobler and purer passion, not only the will, but the highest powers of the intellect, are put in action to gratify it.—But even here, the *essential* part of the function, which consists in the fertilization of the 'germ-cell' by the contents of the 'sperm-cell,' is as completely independent of mental influence, as it is in the plant or in the simplest animal.

105. The function of *Muscular Contraction,* to which nearly all the

sensible motions of the higher Animals are due, is one which has an important connection with almost every one of their vital operations; although, as already explained, this connection is mostly of an indirect character. The property of Contractility on the application of a stimulus is not, however, confined to animals; since it is possessed by many of the Vegetable tissues, and has an important relation with their nutritive processes. Nor, even in animals, is it confined to the muscular tissue. For in the lowest tribes it seems generally diffused through the fabric, and appears to be for the most part excited by external stimuli. But in the higher classes, it is concentrated in a special texture, and is called into operation by a peculiar stimulus, the Nervous power, which originates in the individual itself. By this means it is brought under subordination to the Mind, and is made the instrument of changing the relations between the living organism and the external world.

106. The functions of the *Nervous System* are twofold. First, to bring the conscious Mind (using that term in its most extended sense, to denote the psychical endowments of animals in general) into relation with the external world; by informing it, through the medium of the organs of *sensation*, of the changes which the material universe undergoes; and by enabling it to react upon them through the organs of motion. And secondly, to connect and harmonise different actions in the same individual, without necessarily exciting any mental operation. But, in the words of a profound writer on this subject, "mental acts and bodily changes connected with them, are not merely *superadded* to the organic life of animals, but are intimately connected or interwoven with it; forming, in the adult state of all but the very lowest animals, part of the conditions necessary to the maintenance of the quantity, and of the vital qualities, of the nourishing fluid on which all the organic life is dependent."* In proportion to the complexity and extent of the Psychical endowments of each species of Animals, may their influence over the conformation of the Organic structure be perceived; so that it becomes more and more removed from that which is presented by Vegetables, the chief end of whose existence appears to be the elaboration of an organised fabric from the elements furnished by the inorganic world. In Man, the being that possesses the largest share of these capabilities, the apparatus of Organic life would seem destined for little else than to serve for the maintenance of the Animal functions; the processes of Nutrition being almost entirely directed towards perfecting his Nervo-muscular apparatus, and bringing its functions into most advantageous operation. And it is in him, moreover, that we observe the most unequivocal indications of the direct influence of the Nervous System over the most essential parts of the vital operations; the processes of nutrition and secretion being remarkably modified by states of Mind, especially such as are of an emotional character.

107. In our search for the general laws of the Vital Functions,—or, in other words, for the general plan of Vital Activity,—we shall derive great advantage from keeping constantly in view, that Von Baer's law of *progression from the general to the special* appears to hold good as well in regard to the functional character of organs, as with respect to their

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* Prof. Alison's "Outlines of Human Physiology," p. 13.

structural and developmental conformity; as may be seen in proceeding from the lower to the higher forms of organised being, and in following the successive stages of development of any one of the higher organisms. If we compare the forms which the same instrumental structure presents in different parts of the series, we shall always observe that it exists in its most general or diffused form in the lowest classes, and in its most special and restricted in the highest; and that the transition from one form to the other is a gradual one. The function, therefore, which is at first most general, and is so combined with others performed by the same surface as scarcely to be distinguishable from them, is afterwards found to be limited to a single organ, or to be *specialized* by separation from the rest; these also, by a similar change, having been rendered dependent on distinct organs. Hence the whole work of the organism (so to speak) comes to be accomplished by a 'division of labour' amongst its several organs, each of which is adapted to execute its particular share with a measure of energy and completeness proportionate to the speciality of its development.*

108. Thus, to refer again to the provisions existing in different Plants for the *Absorption* of fluid; we find that this action is performed by the entire surface of the Protophyta, which may be thus said to be *all root;* as we ascend through the series of Cryptogamia, it becomes more and more limited to certain parts of that surface; until in Flowering plants it is chiefly performed by its special organs, the 'spongioles,' or succulent extremities of the root-fibres, which draw-in fluid far more energetically than any portion of the general surface can do. And so in the early development of Phanerogamia, the germ absorbs by its whole surface the nutriment in which it lies embedded; it continues still to absorb by a part of that surface, even after the expansion of its plumula and the extension of its radicle into the soil; and it is not until the store laid-up by the parent has been nearly exhausted, that the proper root-fibres are evolved, which are henceforth to be its special instruments of imbibition. With equal reason the simplest Protophyta might be said to be *all leaf;* their whole surface taking part in those functions, which are restricted, in the higher forms of Vegetable organisation, to the foliaceous appendages. Considered only in reference to its vital operations, therefore, the simplest Plant differs from the most complex, principally in this,—that the whole external surface of the former participates equally in all the operations which connect it with the external world, as those of Absorption, Exhalation, and Respiration,—whilst in the latter we find that these functions are respectively confined to certain portions of the surface. However distinct, therefore, the roots and leaves of a Vascular plant are from each other, they both have a functional analogy with the same simple membrane of the lowest species of Protophyta.

109. Where the greatest degree of specialization of function presents itself, the particular arrangement of the organs will have reference to the general plan of conformation, and to the circumstances under which the being is destined to exist. Thus, whilst the absorbing organs of Plants are prolonged externally into the soil, they are usually distributed in

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* This principle has been frequently and forcibly dwelt on by Prof. Milne-Edwards; who has most fully developed and illustrated it in his "Introduction à la Zoologie Générale," Paris, 1851.

Animals upon the walls of a cavity fitted to retain and prepare the food. Still, the same fundamental unity exists; and the spongiole of the vascular Plant, and the absorbent villus in the Animal, have precisely the same essential character with the membrane which constitutes the general surface of the Sea-weed or of the Entozoon, or which lines the digestive cavity of the Hydra. It may, then, be enunciated as a general truth, that *throughout the whole animated Creation, the functional character of the organs which all possess in common, remains the same; whilst the mode in which that character is manifested, varies with the general plan upon which the being is constructed.* The latter part of this law may be rendered more intelligible by another illustration. The respiratory surface of Plants is always prolonged externally; as they have no means of introducing air into cavities, and of effecting that constant renewal of it which is necessary for the aeration of their nutrient fluid. The same is found to be the case in nearly all aquatic Animals, the gills of which are evidently analogous to the leaves of Plants. In terrestrial Animals, on the contrary, the respiratory membrane is prolonged internally, so as to form tubes or cells exposing a large amount of surface. The different cavities which we find adapted to this office, are all lined by a membrane which is either derived immediately from the external surface, as in Insects, terrestrial Mollusks, &c., or from that inversion of it which forms the digestive cavity, as in Vertebrata; and this membrane is everywhere functionally or instrumentally the same, although the organs of which it forms a part are not homologous, those of one kind often existing in a rudimentary state, where another is fully developed (§ 8).—Throughout the second division of the work, illustrations will be found of this essential unity in the functional character of the different organs common to all; and it need not, therefore, be further dwelt-upon in this place.

110. But it would seem as if, even in the most complex beings, this Specialization of Function seldom proceeds so far, as to incapacitate the more general instrument for taking some part in it; for observation of the functions of the more complex forms of animated beings leads to the knowledge of another law, which is simply an expression of this fact; namely, that *in cases where the different functions are highly specialized, the general structure retains, more or less, the primitive community of function which originally characterized it.** As this principle, also, will be copiously illustrated in subsequent chapters, it is unnecessary here to do more than point out its mode of application; and we shall again refer to the function of Absorption for this purpose. As, in the simplest or most homogeneous beings, the entire surface participates equally in the act of imbibition, so, in the most heterogeneous, every part of the surface retains some capacity for it; since, even in the highest Plants and Animals, the common external integument admits of the passage of fluid into the interior of the system, especially when the supply afforded by the usual channels is deficient. In the same manner we find, that whilst, in the lowest Animals, the functions of Excretion are equally performed by the entire surface, there is in the highest a complex apparatus of Glandular organs, to each of which some special division of that function is assigned;

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* See the Author's Memoir 'On Unity of Function,' in the "Edinburgh Philosophical Journal," July, 1837.

but as all these glands have the same elementary structure, and differ only in the peculiar adaptation of each to separate a particular constituent of the blood, it is in conformity with the law just stated, that either the general surface of the skin, or some of the special secreting organs, should be able to take-on, in some degree, the function of any gland whose duty is suspended; and observation and experiment fully bear out this result, as will hereafter appear (CHAP. IX.)

CHAPTER III.

OF ALIMENT, ITS INGESTION AND PREPARATION.

1. *Sources of the Demand for Aliment.*

111. ALL *Vital Action* involves a *change* in the condition of the Organised Structure which is its instrument.—The vital activity of the Plant is chiefly manifested in its *increase, development,* and *reproduction;* in the multiplication of its component cells, in the metamorphoses which these cells undergo, and in the formation of germs which are destined to be cast off by it, and to originate new organisms elsewhere. These operations can only be performed, however, when the plant is supplied with such alimentary substances, as can be converted by it into the proximate materials of its own tissues; which materials are then appropriated by them, as the *pabulum* at whose expense their growth takes place. In those simple Cellular Plants whose structure is nearly homogeneous throughout, every act of cell-multiplication conduces directly to the growth of the entire mass; since the new cells thus produced remain as constituent parts of it, so long as the organism holds together. In the higher tribes of Plants, however, this is not the case; for we find, as we have seen, that certain organs are periodically developed, the term of whose existence is comparatively brief, so that they only form constituent parts of the structure for a short time, being cast-off as soon as their term of life is over, to be replaced by another set possessing attributes of precisely the same kind. It is, however, through the agency of these temporary organs,—namely, the leaves and the flowers,—that the means of increase and reproduction are provided for the more permanent parts of the organism, which could neither grow nor regenerate its kind without their agency. Thus it would seem to be a general rule, that wherever true *woody* tissue (the production of which seems to be the highest exertion of the vital force of Plants) is produced, the Plant shall be furnished with a set of organs, whose peculiar function it is to prepare and elaborate its materials, accomplishing this with such vigour and activity, that their own vital energy is soon exhausted, so that they die, and are cast-off in a state of decay; and thus the most *permanent* portion of the higher vegetable fabrics is built-up through the instrumentality of the most *transient* part of their organisation, the growth of the wood-cells being entirely dependent upon the vital activity of the leaf-cells. So again, in the higher Plants, we find that instead of that simple liberation of the gene-

rative products from the interior of certain cells, more or less distinctly set-apart from the general structure, which is the common method of fructification in the lowest, a complex apparatus is provided for their evolution; and that this apparatus, —consisting in fact, of elements which might be developed into leaves, and which, though metamorphosed into the parts of the flower, still present an accordance with the general laws of leaf-growth,—is itself of yet more transient duration than the leaves, being cast-off as soon as the germs which it has brought into existence are capable of living separated from the parent structure. Further, we have to note, that it is one part of the office of the apparatus of fructification, to prepare and store-up a supply of nutriment for the early development of the germ; and this store, which makes up the chief bulk of the *seed*, is derived from the materials provided by the roots and leaves of the parent-plant.

112. Thus, then, if we look at the sources of demand for Aliment in the Vegetable Organism, we shall see that they may be reduced to the following heads—I. The *extension of the individual fabric*, by the multiplication and development of its component parts. These may all resemble one another and those from which they sprung (as is the case with the lower Cellular Plants, § 22), may correspond in duration, and may, in their turn, be the subject of further multiplication to an almost unlimited extent; or they may take-on a development which differentiates them from each other, so that whilst some (as the woody bundles in the stems of the Vascular Plants) possess considerable durability, and remain as permanent parts of the fabric, others (as the leaves) are destined for only a temporary activity, replacing for a time those that have already expended their powers and passed through their term of life, and themselves dying as soon as they have completed the same series of phases of existence, which has for its ultimate object the extension of the more permanent parts of the structure.—II. The *production of germs* for the continuance of the race; which not only incorporate in their own substance a certain amount of elaborated nutriment, but which, in the higher plants, carry with them a further supply, at the expense of which their early development takes place.—It is, then, by the activity of the functions of Growth and Reproduction alone, that the demand for food is determined in the Plant; and we shall find that, in their turn, the activity of these functions is dependent upon, and in some degree determined by, the supply afforded to it. Thus it is when the plant is most abundantly furnished with appropriate materials by its roots and leaves, that it will most tend to throw out new leaf-buds, to form new wood, and thus to grow as an individual; whilst, on the other hand, it is when more sparingly supplied with nutriment, that it will produce the greatest number of flower-buds, and develope the most numerous progeny. In the life of the simpler plants, there may be said to be no 'waste' whatever; for so long as their tissues are growing and multiplying, so long do they resist the influences which tend to their decomposition. But in the life of the higher plants, a source of 'waste' arises from the temporary nature of some of their organs; though even this is connected, as we have just seen, with the *constructive*, not with the *destructive* class of operations,—the successional development and death of the leaves being subservient to the building-up of the individual fabric, and to the regenera-

tion of the race. Thus a very large proportion of the aliment taken into the Vegetable system is directly appropriated to these purposes; the amount of carbonic acid and of other excretory matters given off during the period of growth, being very small in proportion to that of the materials introduced; and the fall of the leaves, which restores to the condition of inorganic matter a certain amount of substance that has undergone the organising process, not taking place, until by their instrumentality a considerable addition has been made to the solid fabric of the tree. To these processes of extension and reproduction, there would not seem to be,—at least in a large proportion of the fabrics belonging to the Vegetable kingdom,—any very definite limit.

113. The case is very different, however, as regards the Animal. In it, also the activity of the functions of growth and reproduction becomes a source of demand for food. But, excepting in those tribes which (like Zoophytes) multiply by gemmation, the period of increase is limited. The full size of the body is usually attained, and all the organs acquire their complete evolution, at a comparatively early period. The continued supply of food is not then requisite for the extension of the structure, but simply for its *maintenance;* and the source of this demand lies in the constant 'waste,' to which, during its period of activity, it is subjected. Every action of the Nervous and Muscular systems involves the death and decay of a certain amount of the living tissue, as is indicated by the appearance of the products of that decay in the Excretions; and a large part of the demand for food will be consequently occasioned by the necessity for making good the loss thus sustained. Hence we find that the demand for food bears a close relation to the activity of the 'animal' or *destructive* functions; and thus the Birds of most active flight, and the Mammals which are required to put forth the greatest efforts to obtain their food, need the largest and most constant supplies of nutriment; whilst even the least active of these classes stand in remarkable contrast with the inert Reptiles, whose slow and feeble movements are attended with so little waste, that they can sustain life for weeks and even months, with little or no diminution of their usual activity, without a fresh supply of food.

114. But this waste and decay do not affect the muscular and nervous tissues alone; for as we have found in the Plant, that the higher parts of the structure are developed by the instrumentality of the vital activity of the lower, so do we find in the Animal, that the exercise of those *constructive* operations, by which the materials for the first growth and the subsequent maintenance of the fabric are prepared and kept in a state of the requisite purity, involves the agency of a set of organs, which may be said to be entirely 'vegetative' in their character, and in which, as in the higher Plants, a continual renewal of the cells that constitute their essential structure, seems necessary for their functional activity. Thus all the glandular and mucous surfaces are continually forming and throwing off epithelial cells, whose production requires a regular supply of nutriment; and only a part of this nutriment (that which occupies the *cavity* of the cells) consists of matter that is destined to serve some other purpose in the system, or that has already answered it; the remainder (that of which their solid *walls* are composed) being furnished by the nutritive materials of the blood, and being henceforth altogether lost to

it.—Thus every act of Animal Nutrition involves a waste or decay of Organised tissue, either in the first preparation of the nutrient fluid, or in its subsequent depuration.

115. We may observe a marked difference, however, between the amount of aliment required, and the amount of waste occasioned, by the simple exercise of the *nutritive* or *vegetative* functions in the building-up and maintenance of the animal body, and that which results from the exercise of the *animal* functions. The former are carried on, with scarcely any intermixture of the latter, during fœtal life. The aliment, in a state of preparation, is introduced into the fœtal vessels; and is conveyed by them into the various parts of the structure, which are developed at its expense. The amount of *waste* is then very trifling, as we may judge by the small amount of excretory matter, the product of the action of the liver and kidneys, which has accumulated at the time of birth; although these organs have attained a sufficient development, to act with energy when called-upon to do so. But so soon as the *movements* of the body begin to take place with activity, the waste increases greatly; and we even observe this immediately after birth, when a large part of the time is still passed in sleep, but when the actions of respiration involve a constant employment of muscular power.—In the state of profound *sleep*, at subsequent periods of life, the vegetative functions are performed, with no other exercise of the animal powers than is requisite to sustain them; and we observe that the waste, and the demand for food, are then diminished to a very low point. This is well seen in many animals, which lead a life of great activity during the warmer parts of the year, but which pass the winter in a state of profound sleep, without, however, any considerable reduction of temperature; the demand for food, instead of being frequent, is only felt by them at long intervals, and their excretions are much reduced in amount. And those animals which become completely inert, either by the influence of cold, or by the drying-up of their tissues, do not suffer from the most prolonged deprivation of food; because not only are their animal functions suspended, but their nutritive operations also are in complete abeyance; and as the continual decomposition which would otherwise be taking place in their tissues, is checked by the cold or by the desiccation to which they are subjected, the whole series of changes which would be going-on in their active condition is brought completely to a stand.

116. But there is another most important source of demand for food, amongst the higher Animals, which does not exist either amongst the lower Animals, or in the Vegetable kingdom. Mammals, Birds, and, to a certain extent Insects also, are able to maintain the heat of their bodies at a fixed standard, and are thus made in great degree independent of variations in external temperature. This they are enabled to do, as will be explained hereafter (CHAP. X., Sect. 3), by a process analogous to ordinary combustion; the carbon and hydrogen which are directly supplied by their food, or which have been employed for a time in the composition of their living tissues and are then set free, being made to unite with oxygen introduced by the respiratory process, and thus giving off as much heat as if the same materials were burned in a furnace. And it has been experimentally proved, that the immediate cause of death in a warm-blooded animal from which food has been entirely withheld, is the in-

ability any longer to sustain that temperature, which is requisite for the performance of its vital operations. Hence we see the necessity for a constant supply of aliment, in the case of warm-blooded animals, for this purpose alone; and the demand will be chiefly regulated by the difference between the external temperature and that of the animal's body. When the heat is rapidly carried-off from the surface, by the chilling influence of the surrounding air, a much greater amount of carbon and hydrogen must be consumed within the body, to maintain its proper heat, than when the air is nearly as warm as the body itself; so that a diet which is appropriate to the former circumstances, is superfluous and injurious in the latter; and the food which is amply sufficient in a warm climate, is utterly destitute of power to enable the animal to resist the influence of severe cold. Again, the Bird, whose natural temperature is 110° or 112°, and the bulk of whose body is small in proportion to the surface it exposes, must consume a greater quantity of combustible material for the maintenance of its normal heat, than is required by a Mammal, whose natural temperature is 100°, and whose body, being of much greater bulk, exposes a much smaller proportional surface to the cooling influence of the surrounding medium.

117. Thus we find that, in the Animal body, aliment is ordinarily required for four different purposes; the first two of which are common to it and to the Plant, whilst the others are peculiar to it.—I. The first construction or building-up of the organism, by the development and multiplication of its component parts. II. The production of germs for the continuance of the race; and, in addition, in the female, the provision of the store of aliment required by these germs during their early development. III. The maintenance of the organism both during its period of growth, and after its attainment of its full size, notwithstanding the 'waste' occasioned by the active exercise of the nervous and muscular systems. IV. The supply of the materials for the heat-producing process, by which the temperature of the body is kept up.—The amount required for these several purposes will vary, therefore, not only with the general activity of the nutritive processes, but in accordance with the conditions of the body, as regards exercise or repose, and external heat or cold. It is also subject to great variation with difference of *Age.* During the period of growth, a much larger supply of food is required in proportion to the bulk of the body, than when the full stature has been attained: but this results, not so much from the appropriation of a part of this food to the augmentation of the fabric (the proportion of its whole amount which is thus employed being extremely small), as from the much greater rapidity of *change* in the constituents of the body of the young animal, than in that of the adult; which is evidenced by the large proportional amount of the excretions of the former, by the rapidity with which the effects of insufficiency of aliment manifest themselves in the diminution of the bulk and firmness of the body, by the short duration of life when food is altogether withheld, and by the readiness with which losses of substance by disease or injury are repaired, when the nutritive processes are restored to their full activity. The converse of all this holds good in the state of advanced age. The excretions diminish in amount, the want of food may be sustained for a longer period, losses of substance are but slowly repaired, and everything indicates that the interstitial

changes are performed with comparative slowness; and, accordingly, the demand for food is then much less in proportion to the bulk of the body, than it is in the adult. This contrast is most remarkably shown in the Insect tribes, which are far more voracious in the *larva* than in the *imago* state; many species, indeed, taking no food whatever, after their last metamorphosis; and most others taking very little, except such as they may be preparing to apply to the sustenance of their progeny.

118. The influence of the supply of food upon the size of the individual, is very evident in the Vegetable kingdom; and it is most strikingly manifested, when a plant naturally growing in a poor dry soil is transferred to a rich damp one, or when we contrast two or more individuals of the same species, growing in localities of opposite characters. Thus, says Mr. Ward,* "I have gathered, on the chalky borders of a wood in Kent, perfect specimens in full flower of *Erythræa Centaurium* (Common Centaury), not more than half an inch in height; consisting of one or two pairs of most minute leaves, with one solitary flower: these were growing on the bare chalk. By tracing the plant towards and in the wood, I found it gradually increasing in size, until its full development was attained in the open parts of the wood, where it became a glorious plant, four or five feet in elevation, and covered with hundreds of flowers." We find, then, that by *starvation*, naturally or artificially induced, Plants may be dwarfed, or reduced in stature: thus the Dahlia has been diminished from six feet to two; the Spruce Fir from a lofty tree to a pigmy bush; and many of the trees of plains become more and more dwarfish as they ascend mountains, till at length they exist as mere underwood. Part of this effect, however, is doubtless to be attributed to diminished temperature; which concurs with deficiency of food in producing inferiority of size.—The influence of variations in the supply of food, in producing a corresponding variety of size, seems to be less in the Animal kingdom than in the Vegetable: but this is not because Animals are in any degree less dependent than Plants upon a proper measure of aliment. For such a limitation of the supply as would *dwarf* a Plant to any considerable extent, would be fatal to the life of an Animal. On the other hand, an excess of food, which (under favourable circumstances) would produce great increase in the size of the Plant, would have no corresponding influence on the Animal; for its size appears to be restrained within much narrower limits,—its period of growth being restricted to the early part of its life, and the dimensions proper to the species being rarely exceeded in any great degree. Even in the case of *giant* individuals, it does not appear that the excess of size is produced by an over-supply of food; but that the larger supply of food taken-in, is called-for by the unusual wants of the system,—those wants being the result of an extraordinary activity in the processes of growth, and being traceable rather to the properties inherent in the individual organism, than to any external agencies. The influence of a diminished supply of food, in producing a marked inferiority in the size of Animals, is most effectually exerted during those early periods of growth, in which the condition of the system is most purely 'vegetative.' Thus it is well known to Entomologists, that,

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* "On the Growth of Plants in closely glazed Cases," 2nd edition, p. 16.

whilst it is rare to find Insects departing widely from the average size on the side of excess, dwarf-individuals, possessing only half the usual dimensions, or even less, are not uncommon; and there can be little doubt that these have suffered from a diminished supply of nutriment during their larva state. This variation is most apt to present itself in the very large species of Beetles, which pass several years in the larva state; and such dwarf-specimens have even been ranked as sub-species. Abstinence has been observed to produce the effect, upon some Caterpillars, of diminishing the number of moults and accelerating the transformation; in such cases, the Chrysalis is more delicate, and the size of the perfect Insect much below the average.—That insufficiency of wholesome food, continued through successive generations, may produce a marked effect, not merely upon the stature, but upon the form and condition of the body, even in the Human race, appears from many cases in which such influence has operated on an extensive scale. Of these cases, some of the most remarkable are those of the Bushmen of Southern Africa, and the aborigines of New Holland; whose low physical condition appears to be in great part due to imperfect nutrition.

119. There can be no doubt that the *character* of the food supplied, has an important influence upon the development of *particular parts* of the organism; and may thus modify its general conformation in a remarkable degree. Many of the alterations which are effected by cultivation in Plants, obviously proceed from this source; and when it is known what are the particular components of any special tissue or organ which it is desired to augment, a supply of the appropriate *pabulum* will usually be effectual for this purpose. Thus the production of the Corn-grains is largely increased by azotized manure combined with the earthy phosphates; whilst that of the Sugar-cane is in like manner favoured by non-azotized manure combined with silex. So in the higher Animals, the production of blood-corpuscles is known to be promoted by iron, that of fat by abundance of oleaginous or farinaceous food, and even that of muscle and bone by suitable kinds of diet.—The most remarkable example, however, of the influence of particular kinds of food in modifying the processes of development, is seen in the economy of the Hive-Bee. The *neuters,* which constitute the majority of every community, are really females with the sexual organs undeveloped, the capacity for generation being restricted to the *queen.* If by any accident the queen should be destroyed, or if she be purposely removed for the sake of experiment, the bees choose two or three from among the neuter-eggs that have been deposited in their appropriate cells, and change these cells (by breaking-down others around them) into *royal* cells, differing from them considerably in form, and of much larger dimensions; and the larvæ, when they come forth, are supplied with 'royal jelly,' an aliment of a very different nature from the 'bee-bread' which is stored-up for the nourishment of the workers, being of a pungent stimulating character. After going through its transformations, the grub thus treated comes forth a perfect queen; differing from the 'neuter' into which it would otherwise have changed, not only in the development of the generative apparatus, but also in the form of the body, the proportionate length of the wings, the shape of the tongue, jaws, and sting, the absence of the hollows on the thighs in which the pollen is carried, and the loss of power to secrete wax. Thus

in acquiring the attributes peculiar to the perfect reproductive female, the insect loses those which distinguish the working population of the hive; and of this departure from its usual mode of development, the difference in the food with which it is supplied appears to be the only essential condition.

2. *Nature of the Alimentary Materials.*

120. Amongst the general differences between the Animal and Vegetable kingdoms, none are more striking than those existing between the aliments whereon they are respectively supported, and the mode of their *ingestion* or introduction into the system. The essential nutriment of Plants appears to be supplied by the Inorganic world; and to consist chiefly of the elements of *water*, *carbon*, and *nitrogen*, with certain mineral compounds. The Water is partly derived from the fluid that percolates the soil, which is absorbed by the roots; and partly from the moisture of the atmosphere, which is imbibed by the leaves.—The Carbon is principally obtained (§ 268) from the carbonic acid which exists in the Atmosphere in the proportion of about 0·00049 to 1; but most plants are assisted in their growth by its introduction through the roots also. In all soils of moderate richness, there exists a large quantity of the remains of organised fabrics, the upper layer of which is constantly undergoing some degree of decomposition by contact with the atmosphere, so that carbonic acid is formed in it. The water which traverses such a soil, therefore, will become charged with this gas; and this state of solution appears to be that in which carbon may be most advantageously introduced into the vegetable system. It seems probable that the organic matter which rich soils contain, is not itself applied to the nutrition of the plant, without this previous decomposition;* for it is found that those soils which afford the most steady and equable supply of carbonic acid, are the most favourable to vegetable growth; and that this end may be answered, not merely by an admixture of decomposing organic matter, but by the introduction of substances, such as gypsum or powdered charcoal, which have the property of condensing carbonic acid from the atmosphere.—It is only within a recent period, that the dependence of all Vegetable growth upon a due supply of Nitrogen has been ascertained; but it is now known that, although usually existing in only a small proportion, its presence in the vegetable tissues is peculiarly important at the time of their greatest formative activity; the 'primordial utricle,' which is the seat of the most active vital operations, being composed of albuminous matter, in which nitrogen is an essential ingredient. The small quantity of nitrogen which the usual rate of growth of ordinary Plants causes them to require, appears

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* It has been recently affirmed, by MM. Verdeil and Rislet, that a soluble neutral compound, isomeric with lignin, cellulose, &c., may be extracted from fertile soils; being the result of the partial decomposition of the organised structures at the expense of which these soils have been generated. The solution of this compound in water has a remarkable power of taking up silica and carbonate of lime; and it thus becomes the means of introducing these substances into the plant. According to the chemists who have discovered it, this compound may be directly appropriated as nutriment by growing plants; although they admit that, if not so appropriated, it speedily decomposes and gives off carbonic acid. (See "Comptes Rendus de la Société de Biologie," 1853, p. 111.)

to be derived from the minute proportion of ammonia existing in the atmosphere, in combination with carbonic acid; this being condensed from it in rain or dew, or absorbed in the gaseous state by porous soils, so as in either case to find its way to the roots in the liquid which they imbibe. But the growth of most plants is powerfully stimulated by an additional supply of ammonia, such as they derive from the introduction of decaying animal substances into the soil, as manures; and the efficacy of these is peculiarly manifested in the large increase of the amount of *azotized* compounds, then generated by such plants (the corn-grains, for example) as naturally produce them in considerable proportion.*—To the fertility of a soil, then, it is essential that it yield a sufficient and regular supply of moisture, carbonic acid, and ammonia; the two latter being either attracted from the atmosphere, or evolved by its own decomposition. But however richly a soil may afford these ingredients, it will not support an active vegetation, unless it also supply in sufficient quantity the Mineral substances which Plants require. These are, for the most part, the earthy carbonates, sulphates, and phosphates, the alkaline carbonates, and silica. Most soils contain the greater number of these compounds in larger or smaller proportion; and it is mainly according to the predominance of one or other of them, that particular soils are specially fitted to support those kinds of plants in which a like predominance exists. Thus the Cerealia and Grasses require a large proportion of silica and of the alkaline carbonates; Turnips and Potatoes, more of the alkalies; Peas, Beans, Clover, &c., carbonate and sulphate of lime; while all (but especially the Corn-grains) require a full supply of phosphates.—The opinion that Air and Water, with the inorganic substances they bring with them, furnish the essential food of plants, is confirmed by the fact, that not only will the simpler forms of Lichens appear on barren rocks in the midst of the ocean, increasing by absorption from the atmosphere alone, and preparing by their decomposition a nidus for the reception of the germs of higher orders of vegetation; but that many, even of the more highly organised species, will grow in circumstances where no other kind of nutriment is accessible to them. The small amount of earthy or saline matter contained in the tissues of such plants, must be derived from the atmosphere, which is known to hold such particles in suspension.

121. The only class of Plants which even *seems* to be *dependent* for its support upon matters already organised, is that of *Fungi* (§ 26); but it is probable that this dependence only arises from the peculiarly large and constant supply of carbonic acid and ammonia, which they require

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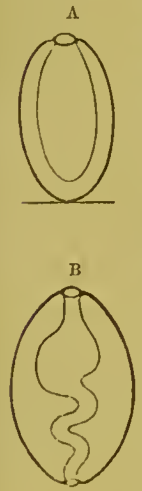
* According to the recent enquiries of M. Georges Ville, the mean quantity of Ammonia contained in the atmosphere is only 22·417 grms. in a million of kilogrammes, (or 0·0000000224 parts); the maximum quantity being 29·43 grms, and the minimum 17·14 grms. He thinks that this quantity is too small to furnish the supply of nitrogen which vegetation involves; and maintains that plants must absorb azote direct from the atmosphere,—an assertion, however, of which no sufficient proof is given. He found that an artificial increase of the ammonia in the atmosphere to an extent of 0·0004, produces an extraordinary increase in the activity of the vegetative processes; and that the plants grown in such an atmosphere contain, when mature, twice as much azote as those grown in pure air. If this treatment be employed at the commencement of the flowering season, the increased development of the leaves checks that of the flowers; and if any flowers are produced they are barren.—("Proceedings of the Royal Society," May 26, 1853.)

as the condition of their growth; as well as (perhaps) from their being only able to appropriate these compounds in the 'nascent' state. There is no reason to believe that they can make use of organic compounds in any other than a state of decomposition, and hence it is that their great utility in the economy of Nature arises; the products of decay, which might otherwise have poisoned the atmosphere, being converted into living and growing tissues.—Fungi present us with two curious analogies to the Animal kingdom; both resulting, no doubt, from the mode in which they receive their aliment. The large quantity of carbonic acid with which their absorbent apparatus furnishes them, prevents the necessity of their drawing any additional supply of it from the atmosphere; but on the contrary, like animals, they have only to get rid of what is superfluous. And again, the proportion of azotized matter contained in their tissues is much greater than in those of any other vegetable; so that their substance, if capable of being digested, is almost as nutritious as animal flesh.

122. It is a general law of vitality, that the materials of nutrition can only be introduced into the living system in the fluid state; and although the ingestion of solid aliment by the higher Animals might seem to contradict such a principle, a little examination into the character of their nutritive apparatus will show that it is framed in conformity with it. In addition to the absorbing organs with which Plants are furnished, and by which they directly imbibe their aliment from the external world, nearly all Animals are provided with cavities for the reception of their food, and for its reduction to a state fit to enter the vessels. The necessity for these cavities arises out of the nature of the aliment required by Animals, which usually pre-exists in a form more or less solid; and also from the occurrence of intervals between the periods at which it is obtained. Whilst the roots of Vegetables are fixed in the soil, and ramify through it in pursuit of their nutriment, Animals, whose locomotive powers are necessary for the search after the food they require, may be said to carry their soil about with them; for their absorbents are distributed on the walls of a digestive cavity, just as those of Plants are externally prolonged into the earth. This cavity is in all instances formed by a *reflexion* of the external surface, of which the *Hydra* (Fig. 34) may be regarded as presenting us with the simplest example. It is merely a bag with one opening (A), which may be regarded as *all stomach.* A higher form is that in which the cavity has two orifices, and thus becomes a canal (B); and all the complicated intestinal apparatus of the higher animals may be considered as a more extended development of this simple type. That the presence of the stomach, however, is not an *essential* character of the Animal (as taught by some Physiologists), but is rather a special adaptation of their organism to the peculiarity of their food, which may be dispensed-with under peculiar circumstances, will appear hereafter (§ 138).—The food which is introduced into this cavity, is acted-upon mechanically by the motion of the walls, and chemically by the secretions poured from their surface; so that the nutritious parts of it are separated from those which may be rejected, and are reduced to a fluid form.—That



the process of Digestion in Animals is really of no higher a character than this, and that it has nothing to do with 'organising' or 'vitalizing' the materials submitted to it, appears alike from *à priori* considerations, and from experiment. For the substances contained in the alimentary canal, and in contact with that reflexion of the external integument which constitutes its lining membrane, are really as much external to the living body, as if they were placed in contact with the skin; we cannot regard them as introduced into it, until they have been absorbed; and up to that period, they hold precisely the same relation to the absorbent vessels, as the fluid diffused through the soil bears to the roots of Plants ramifying upon the surface of that Earth, which has been expressively said to be their 'common stomach.' All the experiments which have been performed upon artificial digestion, have precisely the same bearing; since it appears from them, that if the food be subjected to the action of the same solvent fluids, with the same assistance from heat and from mechanical movement, the result is the same *out of* the stomach as *in* it.

123. The particular articles which constitute the food of the different races of Animals, are as various as the races themselves. Some appear to draw their nutriment from the Inorganic world; but this is not the case in reality. Thus the *Spatangus* and *Arenicola* fill their stomachs with sand, but really derive their nutriment from the minute animals which it contains. The Earth-worm and some kinds of Beetles are known to swallow earth; but they only derive from it the particles of organic matter which it includes, and reject the rest.*

124. Some tribes in almost every division of this kingdom are maintained solely by Vegetable food; and wherever Plants exist, we find Animals adapted to make use of the nutritious products which they furnish, and to restrain their luxuriance within due limits. Thus, the Dugong browses upon the submarine herbage of the tropics; whilst the Hippopotamus roots up with his tusks the plants growing in the beds of the African rivers; the Giraffe is enabled by his enormous height to feed upon the tender shoots which are above the reach of ordinary quadrupeds; the Rein-deer subsists during a large part of the year upon a lichen buried beneath the snow; and the Chamois finds a sufficient supply in the scanty vegetation of Alpine heights. Many species of Animals, especially among the Insect tribes, are restricted to particular Plants; and, if these fail, the race may for a time disappear. But there is probably not a species of Plants, which does not furnish nutriment for one or more tribes of Insects, either in their larva state or their perfect condition, by which it is prevented from multiplying to the exclusion of others. Thus, on the Oak not less than two hundred kinds of Caterpillars have been estimated to feed; and the Nettle, which scarcely any beast will

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* Among the human race, some savage nations are in the habit of introducing large quantities of earthy matter with their food; and this sometimes through ignorant prejudice, but more frequently to give bulkiness to the aliment, so that the stomach may be distended,—as among the Kamschatdales, who mix saw-dust or earth with their train-oil. It has been until recently supposed that the siliceous earth, which has been employed in Lapland in times of scarcity, mixed with flour and the bark of trees, merely answered this purpose; but recent microscopic examination has shown, that it consists of the *exuviæ* of Infusoria, and contains a large portion of animal matter. If the latter be dissipated by incineration, the earth loses about 20 per cent. of its weight.

touch, supports fifty different species of Insects, but for which check it would soon annihilate all the plants in its neighbourhood.—The habits and economy of the different races existing on the same plant, are as various as their structure. Some feed only upon the outside of the leaves; some upon the internal tissue; others upon the flower or on the fruit; a few will eat nothing but the bark; while many derive their nourishment only from the woody substance of the trunk.—It is very curious to observe, that many plants injurious to Man afford wholesome nutriment to other animals; thus, Henbane, Nightshade, Water-hemlock, and other species of a highly poisonous character, are eaten greedily by different races of quadrupeds. Some cattle, again, will reject particular plants upon which others feed with impunity.

125. Every class of the Animal kingdom has its Carnivorous tribes, also, adapted to restrain the too rapid increase of the vegetable-feeders, by which a scarcity of their food would soon be created,—or to remove from the earth the decomposing bodies, which might otherwise be a source of disease or annoyance. The necessity of this limitation becomes evident, if we consider the rapid multiplication which the prolific tendency of the Herbivorous races would speedily create, until checked by the famine that would necessarily result from their inordinate increase. Thus, the myriads of Insects which find their subsistence on our forest trees, if allowed to multiply without restraint, would soon destroy the life that supports them, and must then all perish together; but another tribe (that of the insectivorous Birds, as the Woodpecker), is adapted to derive its subsistence from them, and thus to keep within salutary bounds the number of these voracious little beings. Sometimes, however, they increase to an enormous extent. The pine-forests of the Hartz mountains have been several times almost destroyed by the ravages of a single species of Beetle, the *Bostrichus typographus*, which is less than a quarter of an inch in length; the eggs being deposited beneath the bark; and the larvæ, when hatched, devouring the alburnum and inner bark in their neighbourhood. It was estimated that, in the year 1783, a million and a half of pine-trees were destroyed by this insect in the Hartz alone; and other forests in Germany were suffering at the same time. The wonder is increased when it is stated, that 80,000 larvæ are sometimes found on a single tree. Their multiplication is aided by their tenacity of life; for it is found that, even if the trees infested by these larvæ be cut down, floated in water, kept for a length of time immersed either in water or snow, or even placed upon ice, the grubs remain alive and unhurt. In the pupa state, however, they are more susceptible; and vast numbers perish in this condition from the influence of unfavourable seasons, which operate as the principal check to their multiplication.—A very curious instance of the nature of the checks and counter-checks, by which the 'balance of power' is maintained amongst the different races, is mentioned by Wilcke, a Swedish naturalist. A particular species of Moth, the *Phalæna strobilella*, has the fir-cone assigned to it for the deposition of its eggs; the young caterpillars, coming out of the shell, consume the cone and superfluous seed; but, lest the destruction should be too great, the *Ichneumon strobilella* lays its eggs in the caterpillar, inserting its long tail in the openings of the cone until it touches the included

insect, for its body is too large to enter. Thus it fixes upon the caterpillar its minute egg, which when hatched destroys it.*

126. The Alimentary value of the various substances used as food by the several races of Animals, is not so different as, from the diversity of the sources whence it is drawn, we might be led to suppose. It depends, in the first place, upon the quantity of solid matter they respectively contain; being of course the greater, as the solids form the larger proportion of the entire weight. Many esculent vegetables contain so large a quantity of water, that the nutriment they afford is very slight in proportion to their bulk.—Next, it depends upon the proportion of digestible matter which the solid parts include; for it is not every substance containing the requisite ingredients, that is capable of being reduced to a state which enables it to be absorbed. Thus, woody-fibre is composed of the same elements as starch-gum; but it passes out of the intestinal canal of the higher animals unchanged, and therefore affords them no nutriment; yet there are many tribes of Insects, which seem to draw their supply of nutriment exclusively from wood, and this even in its driest condition. So, again, the horny tissues of animals, though nearly allied to albumen in their composition, are completely destitute of nutritive value to Man and the higher animals, because not capable of being reduced by their digestive process; though certain Insects appear capable of living exclusively upon them.—But when the watery and indigestible parts of the food are put out of consideration, and our attention is directed only to the soluble solids, we find most important relations in the chemical composition of the several alimentary materials, whether furnished by the Animal or the Vegetable kingdom, which render them more or less appropriate to the different purposes that have to be answered in the nutrition of the body. It is the remarkable attribute of Vegetables, that they are enabled to combine the elements furnished by the Inorganic world into two classes of compounds; the ternary, consisting of oxygen, hydrogen, and carbon; and the quaternary, which consist of these elements, with the addition of azote or nitrogen. These two classes are hence termed the *non-azotized,* and the *azotized.*

127. Now the *azotized* compounds which are formed by Plants, are essentially the same with those *Albuminous* substances which are furnished by the flesh and by the nutritious fluids of Animals; and are equally adapted with the latter for the reparation of the waste of the muscular tissue, and for the general nutrition of the body. The quantity of these, however, which Plants yield, is usually small in proportion to that of the non-azotized; being considerable only in the Corn-grains, and in the seeds of Leguminous plants, which the universal experience of ages has demonstrated to be the most nutritious of Vegetable substances. But, unless the food contain a sufficient proportion of these compounds, the body must be insufficiently nourished, and the strength must diminish, even though other elements of the food be in superabundance; and consequently if the food be of a kind which con-

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* The Chapters on the 'Economy of Nutritive Matter' in Dr. Roget's "Bridgewater Treatise," and on the 'Equilibrium of Species' in Sir C. Lyell's "Principles of Geology," may be referred-to for a more extended view of this interesting subject, than the limits of the present work permit.

tains but a small proportion of albuminous matter, a very large amount of it must be ingested, to afford the requisite supply of the essential ingredients. We see a provision for this requirement, in the capacity of the alimentary canal of Vegetable-feeding animals; which is almost invariably far greater than that of the Carnivorous members of the same groups.—There is another azotized compound, *Gelatine*, that is furnished by Animals, to which nothing analogous exists in Plants; this cannot sustain life by itself, and is not an essential article of food; and there is, in fact, much doubt whether it can be applied to the nutrition or reparation of any of the tissues of the body. There is ample evidence that it cannot be transformed into an albuminous compound, so as to be applicable to the nutrition of the muscular and other albuminous tissues. And although the Fibrous substance which constitutes the animal basis of bone, as well as the greater part of tendons, ligaments, skin, mucous and serous membranes, areolar tissue, &c. &c., has the same composition as Gelatine, and might therefore be presumed to be nourished by it when it is employed as food, yet there is adequate evidence that even these tissues are generated in the living body at the expense of the albuminous constituents of the blood; and that, whenever gelatine is introduced into the circulating current, it is speedily decomposed and excreted, serving only (like the non-azotized compounds) to assist in maintaining the heat of the body.

128. The *non-azotized* compounds supplied by Plants, exist under various forms; of which the principal are starch, sugar, and oil. The two former may be regarded as belonging to one class, the *Saccharine* or *Farinaceous;* because we know that starch, and the substances allied to it (such as cellulose, which is the principal constituent of the vegetable tissues), may be converted into sugar by simple chemical processes, and that this transformation takes place readily both in the Vegetable and in the Animal economy. On the other hand, the *Oily* matters are usually ranked as a distinct group of alimentary substances; and it has been maintained that, under no circumstances, has the Animal the power of elaborating fatty matter from starchy or saccharine compounds. But this is now known to be an unfounded limitation; since the transformation of a saccharine into a fatty compound takes place in the case of Bees, which form wax when fed upon pure sugar; and it may be effected also in the laboratory of the Chemist, butyric acid (the characteristic fatty acid of butter) being one of the products of the 'lactic fermentation' of sugar, excited by Animal substances.—Thus, then, whether derived from Vegetable or from Animal bodies, the non-azotized substances available as food are essentially the same. The former kingdom supplies them chiefly in the saccharine or farinaceous form, the latter chiefly in the oleaginous; but a considerable quantity of oil is furnished by certain Plants; and there are Animals which have the power of generating cellulose, like plants, and which store it up in their own bodies. The only Animal tissue to which the non-azotized compounds apparently serve as the appropriate *pabulum*, is the Adipose or fatty: there is reason to believe, however, that oleaginous matter performs a most important part in the incipient stages of Animal nutrition; and that its presence is not less essential to the formation of cells, than is that of the albuminous matter which forms their chief component. If such be the case, it is not

surprising that oil in some form, or substances capable of conversion into it, should be such universal constituents of the food of Animals.

129. Besides serving these purposes, however, the non-azotized compounds have a most important use in warm-blooded Animals; that of supporting the respiratory process, and thus maintaining the temperature of the body. In the compounds of the *Saccharine* group (in which Starch is included), the amount of oxygen is no more than sufficient to form water with the hydrogen of the substance; so that the carbon is free to combine with the oxygen introduced by the lungs, and thus becomes a source of calorifying power. In the *Oily* matters employed as food, the proportion of oxygen is far smaller; so that they contain a large quantity of surplus hydrogen, as well as of carbon, ready to be burned-off in the system, and thus to supply the heat required. The extraordinary power of oleaginous substances to impart heat to the system by the combustive process, is indicated by the experience of the Human inhabitants of frigid zones, who feed upon whales, seals, and other animals loaded with fat, and who devour this fat with avidity, as if instinctively guided to its use. It is through the enormous quantity of this substance taken-in by them, that they are enabled to pass a large part of the year in a temperature below that of our coldest winter, spending a great portion of their time in the open air; as well as to sustain the extremes of cold, to which they are occasionally subjected. And in consequence of its being more slowly introduced into the system than most other substances, a larger quantity may be ingested at one time, without palling the appetite; whilst its bland and non-irritating character favours its being retained until it is all absorbed. In this manner, the Esquimaux and Greenlanders are enabled to consume 20 or 30 pounds of blubber at a meal; and, when thus supplied, can pass several days without food.—On the other hand, among the inhabitants of warm climates, there is comparatively little disposition to the use of oily matter as food; and the quantity of it contained in most articles of their diet is comparatively small.

130. The greatest economy in the use of Aliment is therefore exercised, when the diet contains a sufficient proportion of albuminous substances to repair the 'waste' of the albuminous and gelatinous tissues; and a sufficient amount of non-azotized compounds, to develope (with the aid of other processes) the requisite amount of heat by combination with oxygen. Now in the Milk, which is the sole nutriment of young Mammalia during the period immediately succeeding their birth, we usually find an admixture of albuminous, saccharine, and oleaginous substances; which seems to indicate the intention of the Creator, that all these should be employed as components of the ordinary diet. The Caseine, or cheesy matter, is an albuminous compound; the Butyrine of butter is but a slight modification of the ordinary fats; and the Sugar differs from that in common use, only by its larger proportion of water. The relative amount of these ingredients in the milk of different animals, is subject, as we shall hereafter see, to considerable variation; but they are constantly present in the milk of the Herbivorous Mammalia, and of those which, like Man, subsist upon a mixed diet. It has been recently found, however, that the milk of the purely Carnivorous animals is destitute of Sugar, consisting, like their food, of albuminous compounds and fatty matter only; though even *their* milk is found to contain sugar, when

saccharine or farinaceous compounds have formed part of their diet.—No fact in Dietetics is better established, than the impossibility of long sustaining health, or even life, upon any single alimentary principle. Neither pure albumen or fibrine, gelatine or gum, sugar or starch, oil or fat, taken alone for any length of time, can serve for the due nutrition of the body. This is partly due, so far as the non-azotized compounds are concerned, to their incapability of supplying the waste of the albuminous tissues. But this reason does not apply to the albuminous compounds; which can not only serve for the reparation of the body, but can also afford the carbon and hydrogen requisite for the sustenance of its temperature. The real cause is to be found (partly at least) in the fact, that the continued use of *single* alimentary substances excites such a feeling of disgust, that the animals experimented-on seem at last to prefer the endurance of starvation, to the ingestion of them. Consequently it is quite impossible to ascertain, by such experiments, the nutritive power of the different alimentary principles; no animal being capable of sustaining life upon less than two of them. The same disgust is experienced by Man, when too long confined to any article of diet which is very simple in its composition; and a craving for change is then experienced, which the strongest will is scarcely able to resist. The *natural combinations* in which the alimentary substances present themselves, appear to be those which are best adapted for the healthful nutrition of the animal body.

131. The Organic Compounds, which have been enumerated as supplying the various wants of the system, would be totally useless without the admixture of certain Inorganic substances, which also form a constituent part of the bodily frame, and which are constantly being voided in the excretions, especially in the urine. These substances have various uses in the system. Thus common *Salt* (chloride of sodium) appears to afford, by its decomposition, the *hydrochloric acid* which is concerned in the digestive process, and the *soda* which is an important constituent of the bile. Its presence in the serum of the blood, also, and in the various animal fluids which are derived from this, aids in keeping in solution the organic constituents of these fluids, and in preventing their decomposition.—The *Carbonates* and *Basic Phosphates* of *Potass* and *Soda* are most important constituents of the blood; and potass is also an essential component of muscular tissue.—*Phosphorus* seems to be chiefly requisite as one of the materials of the nervous tissue; and also, when acidified by oxygen and united with lime, forms the bone-earth by which bone is consolidated.—*Sulphur* exists in small quantities in several animal tissues; but its part appears to be by no means so important as that performed by phosphorus.—*Iron* is an essential constituent of hæmatine; and is consequently required for the production of the red corpuscles of the blood in Vertebrated animals.—*Lime* is required for the consolidation of the bones of Vertebrata, and for the shells and other hard parts that form the skeletons of the Invertebrata; and it exists in the animal body in combination either with carbonic or with phosphoric acid. The Carbonate would seem principally destined to mechanical uses only; and we find it predominating, or existing as the sole mineral ingredient, in those non-vascular tissues of the Invertebrated animals, which give support and protection to their soft parts. The amount of production of these tissues depends in great part upon the supply of carbonate of lime which the animals receive.

Thus the Mollusca which inhabit the sea, find in its waters the proportion of that substance which they require; but those which dwell in streams and fresh-water lakes that contain but a small quantity of lime, form very thin shells; whilst the very same species inhabiting lakes, which, from peculiar local causes, contain a large impregnation of calcareous matter, form shells of remarkable thickness. The Crustacea, which periodically throw off their calcareous envelope, are enabled to renew it with rapidity, by the appropriation of a store of material previously laid-up in the coats of the stomach. The large amount of carbonate of lime which is required by the laying Hen, is derived from chalk, mortar, or other substances containing it, which she is impelled by her instinct to eat; and if the supply of these be withheld, the eggs which she deposits are soft on their exterior, having the fibrous element of the shell unconsolidated by any intervening deposit of calcareous particles.

132. These substances are contained, more or less abundantly, in most of the articles generally used as food; and where they are deficient, the animal suffers in consequence, if they be not supplied in any other way. —Common *Salt* exists, in no inconsiderable amount, in the flesh and fluids of animals, in milk, and in the substance of the egg; it is not so abundant, however, in Plants; and the deficiency is usually supplied to herbivorous animals from extraneous sources. Thus, salt is purposely mingled with the food of domesticated animals; and in most parts of the world inhabited by wild cattle, there are spots (such as the "buffalo-licks" of North America) where it exists in the soil, and to which they resort to obtain it.—The *Alkaline Bases* are supplied both by Vegetable and by Animal food; what is drawn from the former, however, is usually combined with some organic acid, which is decomposed within the animal body; where also is generated, by the oxidation of phosphorus, the phosphoric acid that is found in combination with them.—*Phosphorus* exists also, in combination with albuminous compounds, in all animal substances composed of these; and in the state of phosphate, combined with lime, magnesia, and soda, in many substances, both vegetable and animal, ordinarily used as food.—*Sulphur* is found in union with albuminous compounds, in flesh, eggs, and milk; also in several vegetable substances; and, in the form of sulphate of lime, in most of the river and spring water used as drink.—*Iron*, also, is very generally diffused, in small quantity, through the tissues of plants; but it exists in much larger proportion in the flesh, and more particularly in the blood, of animals; and it appears from comparative analyses of the blood of Carnivorous and Herbivorous Mammals, that the proportion of red corpuscles, and consequently of iron, is greatest in the former; which circumstance seems partly attributable to the nature of their diet.—*Lime* is one of the most universally diffused of all mineral bodies; for there are very few Animal or Vegetable substances, in which it does not exist. The principal forms in which it is an element of Animal nutrition, are the carbonate and phosphate. Both these are found in the ashes of the grasses, and of other plants used as food; the phosphate of lime being particularly abundant in the corn-grains. Phosphate of lime unites readily with albumen, caseine, &c.; and a large quantity of it is contained in the milk of the Mammal, and in the egg of the Bird.

133. The dependence of Animal life upon a constant supply of aliment,

is more close in some cases than in others. As a general rule it is the most immediate, when the vital processes, particularly those of Nutrition, are being most actively performed. Thus, we find that young animals are never able to bear the deprivation of food to the same extent with older ones of the same species; and that the warm-blooded Vertebrata—viz. Mammals and Birds,—are usually less capable of abstinence than Reptiles and Fishes. Even of the first of these classes, however, many species pass several months without eating, during the state of hybernation; whilst among many cold-blooded animals, the period of abstinence from food may be indefinitely prolonged, under the influence of those agencies which keep them in a state of complete torpidity or 'dormant vitality'. (See GENERAL PHYSIOLOGY).—When we carry our enquiries further, however, it becomes difficult to give any general explanation of the varieties which we meet-with in this respect, among the different species of animals. Thus, it has been observed by Flourens and Dugès,* that the Mole perishes, when in a state of confinement, if not fed every day, or even more than once a day; whilst the Dog has lived without food for 36 days, the Antelope and the Wild Cat for 20, and the Eagle for five weeks. It is in Reptiles, that the power of abstinence appears to exist to the greatest extent among Vertebrata. Putting aside those cases in which the natural period of torpidity has been artificially extended, we find numerous instances in which these beings have performed all the functions of life for many months together, without the ingestion of food; Tortoises, Lizards, Serpents, and Batrachians all seeming to agree in this respect. It is to be borne in mind, however, that a large supply of food is frequently ingested at once by these animals; and, that, owing to the slowness of their digestive process, the introduction of the aliment into the system is protracted over a very long period,—as is seen, for example, in the case of the *Boa constrictor*, which occupies a month in the digestion of a single meal. Little is known regarding the powers of abstinence possessed by Fish; but it has been stated that some of this class, such as the Perch, naturally take food but once a fortnight.†—It is perhaps among the Insect tribes, that we find the power of sustaining a deprivation of aliment the most remarkably evidenced. The Scorpion has been known to endure an abstinence of three months, the Spider of twelve months, and the *Scarabæus* beetle of three years, without inconvenience or loss of activity; the *Melasoma*, also one of the beetle tribe, has lived for seven months pinned-down to a board. We notice in the class of Insects a very striking illustration of the general fact already stated, respecting the difference between the old and the young animal of the same species. The Larva is not only extremely voracious, but is usually incapable of sustaining a long abstinence; whilst in many tribes the Imago never eats, but dies as soon as its share in the propagation of the race is accomplished.—From what is known regarding the power of abstinence in the Mollusca, it may be stated generally, that they are not capable of maintaining their activity if not frequently supplied with food, in this respect corresponding with the larvæ of Insects; but that, when reduced to a state of torpidity, whether by cold or by the deprivation of food, they may sustain life without any aliment for a very protracted period.

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* "Physiologie Comparée," tom. ii. p. 288.

† Gold-fish have been known to live and thrive in small vessels of water, without any perceptible nutriment, for two or three years. But, if they be not fed in any other way, it is requisite that the water they inhabit should be frequently changed; and the minute quantity of organic matter which it holds in solution, is probably the source of their aliment.

134. Some have attempted to show that Herbivorous animals are more dependent upon a constant supply of food, than Carnivorous species; and that domesticated animals less easily sustain a deprivation of it, than wild ones. But these statements, though generally true, are found to be wanting in accuracy when applied to individual cases. It would probably be more correct to state, that, in proportion to the facility with which each species usually obtains its food, will be the directness of its dependence upon this, and its inability to sustain a protracted abstinence. In accordance with this principle, we observe that, though vegetable-feeders have in general their food within reach, and are very dependent upon its constant supply, some, as the Camel, are enabled to sustain abstinence better than many Carnivorous species; and that some carnivorous animals, being enabled from the nature of their food to obtain it with little difficulty, are comparatively unable to bear the want of it. On the same principle it is evident that domestication may induce a change in the character of the animal, in this respect, as in others, by causing it to become accustomed to frequent or constant supplies of food.—A like adaptation may be found among the Larvæ of Insects. Those which feed upon vegetables or upon dead animal matter, speedily die out of the reach of their aliment; whilst those that lie in wait for living prey, the supply of which is uncertain, are able to endure a protracted abstinence, even to the extent of ten weeks, without injury.*

135. The general facts which appear to have been substantiated, in regard to the mode in which the Animal body is sustained by Food, may be thus summed up :—

I. The waste of the tissues of which *Albumen* or *Gelatine* is the basis, must be supplied by Albuminous compounds, whether these be derived from the Animal or from the Vegetable kingdom; the amount of this 'waste,' and consequently the demand for albuminous aliment, depends essentially upon the degree of vital activity which has been put forth, and especially upon the exercise of the nervo-muscular apparatus; and therefore, *cæteris paribus*, it is greater in cold-blooded animals in proportion to the *elevation* of the external temperature.

II. The materials of the *Adipose* tissue, and the oleaginous particles which seem requisite in the formative operations of the system generally, are derived in the Carnivorous races, from the fatty substances which the bodies of their victims may contain; whilst the Herbivorous not only find them in the oleaginous state in their food, but have the power of producing them by the conversion of farinaceous and saccharine matters.

III. The foregoing statements are applicable to all tribes of Animals, 'cold-blooded' as well as 'warm-blooded;' we have now to consider the special case of the latter.—In the *Carnivorous* tribes the 'waste' of the tissues is so great, in consequence of the restless activity which is habitual to them, that it appears to furnish a large proportion of the combustible material required for the maintenance of their proper temperature. The remainder is made-up by the fat of the animals upon which they feed; and it is to be observed that the amount of this is much greater in the bodies of animals inhabiting the colder regions of the globe, than in the inhabitants of tropical climates.—In the *Herbivorous* tribes, the case is different. They are, for the most part, much less active; and the 'waste' of their tissues consequently takes place in a less rapid manner, and is far from supplying an adequate amount of combustible material, especially in cold climates. Their heat is in great part sustained by the combustion of the saccharine and oleaginous elements of their food, which are appropriated to this purpose without having ever formed part of the living tissues; and the demand for these will be larger in proportion to the *depression* of the external temperature, a greater generation of caloric being then required to keep-up the heat of the body to its proper standard.

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* Lacordaire, "Entomologie," tom. ii. p. 152.

IV. Hence 'cold-blooded' animals can usually sustain the privation of food longer than warm-blooded; and this more especially when they are kept *cool*, so that they are made to *live slowly;* and death, when at last it does ensue, is consequent upon the general deficiency of nutrition. On the other hand, 'warm-blooded' animals, whose temperature is uniformly high, must always *live fast;* and deprivation of food is fatal to them, not only by preventing the due renovation of their tissues, but also by destroying their power of sustaining their heat. The duration of life under these circumstances depends upon the amount of fat previously stored-up in the body, and upon the retardation of its expenditure by external *warmth*, or by the enclosure of the body in non-conducting substances; and there is evidence that, if this be duly provided for, and all unnecessary waste by nervo-muscular activity be prevented, the life even of a warm-blooded animal may sometimes be prolonged for many weeks without food.

3. *Ingestion and Preparation of Aliment in Plants.*

136. Although, as already explained, the Vegetable world as a whole is supported by the introduction of the alimentary materials derived from the Earth and Air into the organism, without any preliminary alteration, yet there are particular cases in which adaptations of structure are met with, that appear to be subservient to the reception and preparation of nutritive materials; and some of these it would not be easy to exclude from any definition we might frame of a 'stomach.' Concavities in different parts of the surface, fitted for the collection of the moisture caught from rain or condensed from dew, may frequently be observed; and these vary in the complexity of their structure, from the simple depressions in the leaves of the *Tillandsia* (wild pine of the tropics) or of the *Dipsacus* (teasel), to the extraordinary *ascidia* of the 'Pitcher-plants.' The exact method in which the fluid thus obtained is applied to the nutrition of the plant, is not always evident.* Sometimes the channelled leaves seem to convey it to the roots, by which it is absorbed in the usual manner. In

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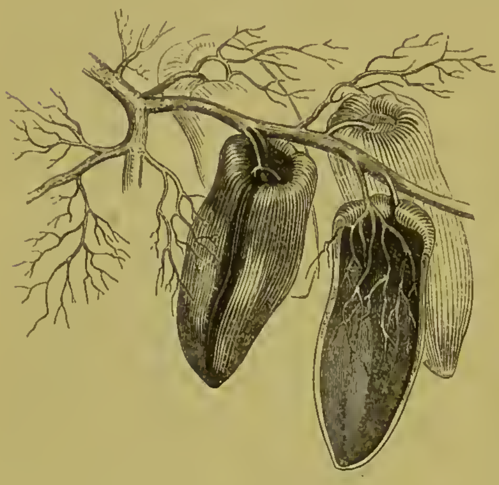
* It is difficult to ascertain how much of the fluid which the pitcher of the *Nepenthes* or 'Chinese pitcher-plant' contains, is collected from the atmosphere by the downy hairs that line its interior, and how much is secreted by the plant itself; and it is certain that the young pitcher contains fluid secreted from an organ within it, before its lid first opens.

FIG. 89.



Pitchers of *Dischidia Rafflesiana*, with tufts of rootlets prolonged from neighbouring branches; *a*, pitcher cut open, to show the ramification of the rootlets in its interior.

the *Dischidia* (Fig. 89), on the other hand, the fluid collected by the pitchers seems destined to be more directly appropriated by the plant, through an absorbing apparatus provided for that purpose. This curious plant grows by a long creeping stalk, which is bare of leaves until near its summit; and as, in a dry tropical atmosphere, the buds at the top would have great difficulty in obtaining moisture through the stem, a sufficient supply is provided by the pitchers, which store up the fluid collected from the occasional rains. "The cavity of the bag," says Dr. Wallich,* "is narrow, and always contains a dense tuft of radicles, which are produced from the nearest part of the branch, or even from the stalk on which the bag is suspended, and which enter through the inlet by one or two common bundles. The bags generally contain a great quantity of small and harmless black ants, most of which find a watery grave in the turbid fluid which frequently half-fills the cavity, and which seems to be entirely derived from without." Thus it would seem as if the failure of the ordinary means of support in this curious Plant, has been compensated by the addition of an organ, which like the stomach of Animals, serves as a receptacle for the supplies it may occasionally obtain.—According to Mr. Burnett,† in the pitcher of the *Sarracenia*, a process still more like that of animal digestion goes on; for it appears that the fluid it contains is very attractive to insects, which, having reached its surface, are prevented from returning by the direction of the long bristles that line the cavity. The bodies of those which are drowned seem, in decaying, to afford a supply of nutriment that is favourable to the growth of the plant; like the similar process on the leaves of the well-known *Dionœa muscipula* (Venus' fly trap), to the health of which a supply of animal food appears to be essential.—Although such instances as these may seem to contradict the general statement, that Plants derive the materials of their nutrition from the inorganic world, yet they probably do so more in appearance than in reality. In all cases where previously organised matter influences their growth, it seems to do so only whilst in a decomposing state, during which it is separated into its ultimate elements or into very simple combinations of them. In Animal digestion, on the contrary, the proximate principles contained in the food appear to be immediately subservient to the formation of others of a higher order; and whatever tendency to disunion their elements might have previously manifested, this is immediately checked by the antiseptic qualities of the gastric fluid.

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* "Plantæ Asiaticæ Rariores," vol. ii. p. 35.

† "Brande's Quarterly Journal of Science," vol. vi.

4. *Ingestion and Preparation of Aliment in Animals.*

137. In considering the various organs which Animals possess for the *in*gestion and *di*gestion of their food, it is right to take notice, in the first instance, of those cases in which there appears to be an absence of that provision for its reception, which is on the whole so characteristic of the beings included within the limits of this kingdom.—There are several examples, even amongst animals of high organisation, in which, during the last stage of their evolution, there is an entire absence of any power of receiving nourishment into the system. These are principally met-with in the class of *Insects;* among which there are many that take no food in their perfect or *Imago* state, the duration of this being very short, and serving merely for the performance of the reproductive act. In some of these cases, the mouth appears to be actually closed, although the digestive apparatus remains, but in an atrophied condition: in all, however, the appropriation of food has been actively performed during a previous stage of the animal's existence. But an animal has been recently discovered, which takes-in no nutriment, from the time of its quitting the egg, until its death, and which does not possess either oral orifice or digestive cavity; this is the *male* of the curious *Notommata* described by Mr. Dalrymple,* which, being entirely incapable of deriving support from the nutriment upon which the female subsists, has no apparent means of increase or maintenance, after it has exhausted the store prepared for it in the egg; and it is probable that the duration of its life is extremely limited, and that it ceases to exist soon after it has performed its part in the reproductive function.—Such instances are not really so exceptional as they at first sight appear; we have now to consider those cases, in which the growth and development of beings included in the Animal kingdom take place at the expense of aliment appropriated by themselves; and in which there is, nevertheless, no semblance of a digestive cavity for its reception.

138. *Agastric Animals.*—The only Animals which can be properly said to be nourished by imbibition solely, without some previous operation of a digestive character, are the *Cestoid Entozoa* (Tapeworm, &c.); which, according to the most recent and accurate researches, are not only unpossessed of a mouth, but also of anything equivalent to a gastric cavity or intestinal tube.† These creatures are supported by the juices of the animals which they infest; and as the softness of their bodies fits them to imbibe these through their whole external surface, no more special organization appears to be necessary. The transition from these to the unicellular Protozoa is made by the curious *Gregarina,*‡ the simplest Entozoon known; being a single cell, usually more or less ovate in form, sometimes considerably elongated, with a beak or proboscis (often furnished with a circular row of hooklets) projecting from one extremity.

139. *Unicellular Animals.*—The condition of those simple Protozoa in which every cell is an independent 'zooid,' in regard to their mode of receiving and appropriating food, is so peculiar as to require special notice. Although they are destitute of any proper digestive cavity for

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* "Philosophical Transactions," 1849, p. 331.

† See Van Beneden's Memoir "Les Vers Cestoïdes," Brussels, 1850; and Siebold 'Uber den Generation's-wechsel der Cestoden' in "Siebold and Kölliker's Zeitschrift," 1850.

‡ See Kölliker, in Siebold and Kölliker's Zeitschrift, Bd I., 1848.

the reception of aliment, the particles from which they derive their nutriment are nevertheless introduced into the very midst of their own substance; and are subjected there to an operation that is not less truly *digestive,* than that which is performed within a regular stomach. This is effected in one of two modes: either by the passage of the food from the exterior to the interior at any point indiscriminately; or by its admission through a definite and constant opening in the cell-wall, which may be considered as a mouth.—Of the former method we have a characteristic example in the *Actinophrys,* whose vital economy has been attentively studied by Prof. Kölliker.* This animal consists of a homogeneous jelly-like, contractile substance, very soft and delicate in its consistence; it has no distinct enveloping membrane, and does not present the slightest trace of mouth, stomach, intestine, or anus. Throughout this substance, but more particularly near its surface, there are observed *vacuoles* or spaces occupied only by fluid; these have no definite boundaries, and may be easily made artificially either to coalesce into larger ones, or to subdivide into smaller. The outer layer extends itself into contractile tentacular filaments (pseudopodia), whose substance is the same as that of the rest of the body, only differing from it in having no vacuoles. Notwithstanding the simplicity of its structure, this creature feeds not merely upon minute Algæ, but even upon active Animalcules, the young of Crustaceans, &c.; any of these, when they happen to come in contact with one of the tentacular filaments, being usually retained by adhesion to it. As this filament shortens itself, all the surrounding filaments apply themselves to the captive particle, bending their points together so that it gradually becomes enclosed, and gradually shortening so as at last to bring the prey close to the surface of the body. The spot with which it is brought into contact, then slowly retracts, and forms at first a shallow depression, gradually becoming deeper and deeper, into which the prey sinks, little by little; for some time, however, continuing to project from the surface. The depression at last assumes a flask-like form, by the drawing-in of its margin; and finally its edges close together, and the prey is entirely shut-in. This gradually passes towards the central part of the body, where its soluble parts are dissolved; whilst, in the mean time, the external portion of the body recovers its pristine condition. Any indigestible residue, as the shell of a Crustacean, or the case of a Rotifer, finds its way to the surface of the body, and is extruded from it, by a process which is precisely the converse of the preceding. Thus a mouth, stomach, and anus, are formed as it were extemporaneously, on every occasion on which food is to be ingested; and this process is mainly effected by the contractility of the soft homogeneous tissue of the body. The number, as well as the size, of the particles included by the Actinophrys at any one time, is very various; frequently there are more than ten or twelve.†—It is probable that the *Amœba* (Fig. 33) and the *Rhizopoda* in general obtain their food by a very similar process; since particles like those which afford nutriment to Actinophrys are frequently perceived to be (as it were) imbedded in the substance of their bodies; which seem, equally with it, to be destitute of any regular orifices of entrance or exit, or any uniform definite cavity.

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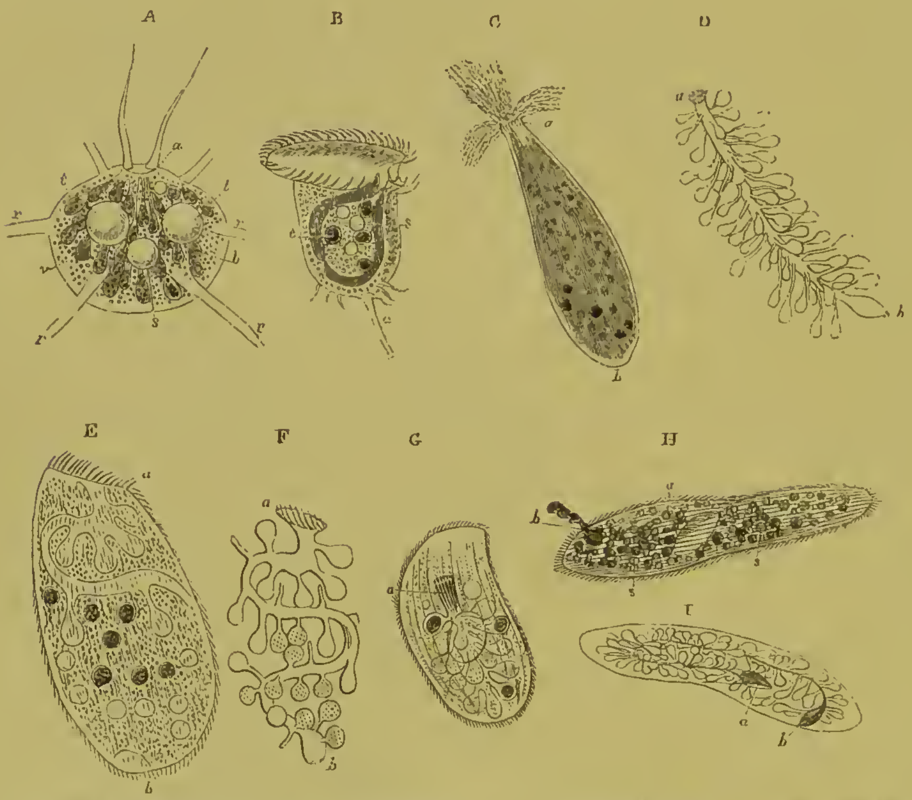
* "Siebold and Kölliker's Zeitschrift," Band I., p. 198; translated in the "Quarterly Journal of Microscopical Science," vol. i., p. 25.

† The process above described, like the structure of the animal, was altogether misconceived by Prof. Ehrenberg; who has described this creature as possessing a regular mouth and anus, and a multitude of stomachs.

140. Among the *Infusory Animalcules*, however, we find individualized cells, composed of the same kind of substance with the Rhizopods, receiving aliment into their interior by a definite oral orifice; as well as, in many instances, rejecting indigestible or excrementitious matters through an anal outlet. The existence of an orifice directly leading into the cavity of the cell which constitutes the entire body, and usually surrounded by a fringe of cilia, is probably to be regarded as the special character of this class; distinguishing it alike from the Vegetable organisms which have so strong a superficial resemblance to it, and from the Rhizopods with which it is in other respects so nearly allied. To this class (which was made by him to include not merely the Rhizopods, but also a large number of Vegetable forms) Prof. Ehrenberg gave the designation of *Polygastrica*, as expressing what he considered to be the peculiar feature of their organisation; namely, the presence of a number of stomachal cavities in the interior of the body, usually connected together by an intestinal tube, as represented in Fig. 90. It is now almost universally considered, however, among unprejudiced observers, that this view is altogether wrong; no such canal or system of stomachs being proved to have any real existence; and the appearances which gave rise to the supposition, being capable of another and a far more self-consistent explanation. It is one of the most remarkable proofs of the invalidity of Professor Ehrenberg's views on this point, that among the beings which he most confidently described and figured as possessing definite stomachs, are many which have been since found to be undoubtedly Plants; such, for example, as the *Volvox-monad*, Fig. 90, A. The truth appears to be simply, that the bodies of these animals resemble those of *Actinophrys* or *Amœba*, as regards the nature of the substance of which they are composed (which has received the designation of Sarcode); the principal difference being, that the external envelope is more completely differentiated from its contents; so that, being prevented by its superior firmness from making their way to the interior of the body through any point of its parietes, the particles of aliment find a definite orifice prepared for their reception. Into this orifice they are driven by the action of the cilia which fringe it (Fig. 90, B, C, E), or (more rarely) are drawn by a set of prehensile filaments that are set round it (G, *a*); and they are then admitted to the general cavity of the body (cell). When several particles of extreme minuteness are thus introduced (such, for example, as fine particles of indigo or carmine diffused through the water in which the animalcules are living), they seem very commonly to be retained in a little globular cavity immediately within the mouth, where they are pressed into a degree of consistence sufficient to hold them together as minute pellets that take the shape of their mould. When a pellet has been thus formed, it is expelled into the general cavity of the body, and the formation of another globular mass commences. As one after another is thus forced-in, each, as it is introduced, pushes-on the rest; and a kind of circulation of the globular pellets is thus occasioned, those first formed making their escape (after yielding up

their nutritive materials) by the second orifice.* Sometimes, however, the body ingested may be of far larger dimensions than the globular pellets thus formed, one Animalcule being occasionally seen to swallow another nearly as large as itself,—a fact which seems of itself almost sufficient to negative the 'polygastric' hypothesis. It is in the ingestion of such bodies, that the circlet of bristle-like filaments round the mouth (designated by Prof. Ehrenberg as 'teeth') becomes especially useful; for they first expand to receive the morsel, and then contract behind it, so as to push it onwards into the orifice.

FIG. 90.



Polygastric Animalcules according to Ehrenberg:—A, individual monad of *Volvox globator*, showing *a*, the supposed mouth; *b*, *b*, gastric vesicles; *s*, *t*, *t*, contractile vesicles; *r*, *r*, *r*, cords of communication;—B, individual of *Vorticella citrina*; *a*, the stalk; *s*, contractile vesicles; *t*, intestinal tube;—C, external aspect of *Enchelis pupa* in the act of taking food, showing *a* the mouth, and *b* the anal orifice;—D, supposed digestive apparatus of the same animalcule; E, F, similar views of *Leucophrys patula*; G, *Chilodon cucullulus*; showing *a* the dental apparatus; H, I, *Paramecium aurelia*, showing *a* the mouth, *b* the anus, *s* contractile vesicles.

141. The transition from the Unicellular animals, in which, however great the aggregation, every cell repeats the rest, to those higher organisms in which the parts of the aggregate mass are completely differentiated from each other, is effected (as already pointed out, § 35) through the group of Sponges; and in no part of the structure is this transition more evident, than it is in the provision for the reception of food. For a mass of Sponge may be regarded, on the one hand, as an aggregation of Amœba-

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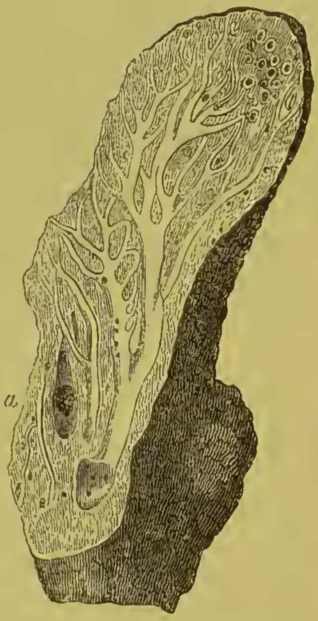
* See Prof. Meyen, in "Ann. of Nat. Hist.," Vol. III., pp. 100 and 170. The author is able to confirm Prof. Meyen's account as to all essential particulars, from his own observations.

like cells, each one living for and by itself, but all being held together by a common integument, and supported by a framework which all participate in forming. Or, on the other, it may be looked-at as a whole, and the attention chiefly fixed upon the system of canals which traverses the body, and upon the circulation of fluid that goes-on within these, by the agency of the cilia with which they are lined. These canals must be considered as altogether forming an alimentary cavity, which is so extended through the mass, as to supply to every part of it the materials of its growth; whilst the manner in which the several Sponge-cells draw their aliment from the circulating current, finds its exact parallel in the manner in which the individual cells that enter into the composition of the most highly-organised fabric, nourish themselves by imbibition from the fluid that bathes their exterior (§ 166).

142. *Polystome Animals.*—In all animals whose entire bodies are repeated by the process of gemmation (§ 34), but whose digestive cavities remain in connection with one another, the entrance to each division of the stomach is properly to be accounted a distinct mouth; and thus the entire composite fabric may be said to be 'polystome' or many-mouthed. This is the case amongst all the 'composite' Zoophytes, whether *Hydraform, Actiniform,* or *Alcyonian* (§§ 151, 152): and by that early form of the spongoid basis of the latter (Fig. 91), in which the polypes are not yet developed at the extremities of the canals, we are carried back to the true Sponges, in which the canals never become furnished with polypes. It is equally the case among the *Composite Acalephæ,* whose strange forms, it is now satisfactorily determined, are the result of a process of gemmation, which multiplies the entrances to the complex digestive cavity, that extends continuously (as in the Hydroid Zoophytes) through all the parts thus produced.*—There is no known instance of a multiple mouth in any other animals than such as thus acquire a composite structure; for the *Rhizostoma* (Fig. 92) does not constitute a real exception. In this animal, though formed upon the general plan of the Medusæ, we find, in place of

Fig. 91.



Portion of a young branch of the polypidom of *Alcyonium stellatum,* divided longitudinally to show the spongiform character of its structure; *a,* incipient state of young polype.

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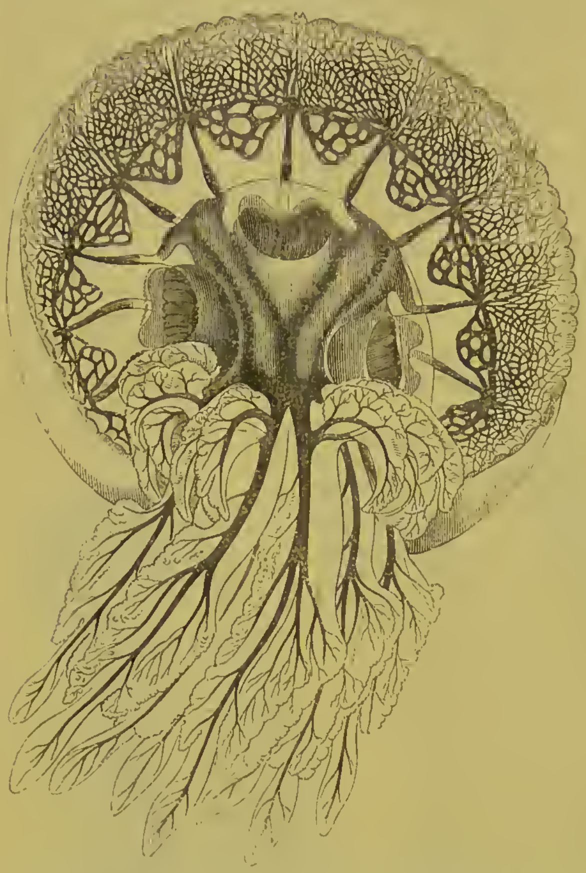
* This very important modification of the views formerly entertained regarding the *Physograde, Cirrhigrade,* and *Diphyd* Medusæ, has been brought about by the researches of Mr. T. H. Huxley communicated to the Royal and Linnæan Societies in 1849; by those of Dr. Rudolf Leuckart, published in "Siebold and Kölliker's Zeitschrift," 1851, and in his Monograph of the Siphonophoræ in his "Zoologische Untersuchungen," 1853; and by those of Prof. Kölliker "Die Schwimmpolypen oder Siphonophoren von Messina," 1853.—It is much to be regretted that the delay in the publication of Mr. Huxley's Memoir on the Physophoridæ and the Diphydæ, on the part of the Linnæan Society, should have deprived him of the credit to which he is entitled, as the original enunciator of the correct idea of the nature of these perplexing forms.

an open mouth in the centre of its eight tentacula, the tentacula themselves excavated by canals, which communicate with the single cavity of the stomach, and which ramify and subdivide, until their finest branches open on the surface by pores that are too small to allow any save very minute Animalcules to enter. But, as Eisenhardt has shown,* the Rhizostoma differs from other animals only in this; that its mouth (which is really single) does not open directly outwards, but is provided with a number of tubular appendages, which extend themselves into the foliaceous expansions of the arms, so as to augment, as much as possible, the number of points through which the alimentary particles required by this animal may be absorbed.—Here, then, we have a sort of transitional form between the composite 'polystome' Acalephs, and those 'monostome' tribes which correspond with all higher animals in possessing but a single external entrance to the digestive cavity.

Fig. 92.



Rhizostoma injected with coloured fluid, to show the central digestive cavity, and the canals branching-off from it to ramify in the arms and in the disk.

143. *Oral Apparatus.*—The relative size and form of the single oral orifice that is common to all other animals, differ very greatly, according to the nature of the food upon which the species is destined to live. The Invertebrate division contains many groups, that are supported by *suction* of the juices of higher animals or of plants; and in them we usually find the oral orifice narrowed and sometimes immensely prolonged. As such a means of obtaining food usually involves the necessity of locomotive powers, whereby the animal may go in search of it, we find, as might be expected, that it is most common in the Articulated sub-kingdom; all the principal classes of which,—Entozoa, Annelida, Insects, Crustaceans, and Spiders,—contain groups of greater or less extent, which are especially adapted for obtaining their food by suction. The *Pycnogonidæ* (Fig. 105) present a characteristic example of the most simple form of suctorial mouth, in which the aperture is merely narrowed and somewhat prolonged;† but the most remarkable modifications for this purpose are to

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* "Nova Acta Leopold," tom x. p. 392.

† From the situations in which these creatures are commonly found, the Author would infer that they draw their nourishment from the mucus that covers the surface of seaweeds.

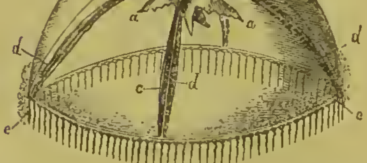
be met-with in the class of Insects, especially in the *Lepidopterous* and *Dipterous* orders. Of the first of these groups, a considerable proportion feed upon the juices of flowers, which the large expanse of their wings prevents them from entering; and their long *haustellium*, which is coiled up beneath the head when not in use, can be so extended as to suck up the honey from the bottom of a deep blossom, while the insect rests upon its outer edge. Of the latter, however, a considerable proportion feed upon the juices of animals; but there are some that have recourse to the honeyed exudations of flowers; and among these the *Nemestrina longirostris* (a Dipterous insect of the Cape of Good Hope) deserves especial mention, the length of its proboscis being about 3 *inches*, whilst that of its body is only about 8 *lines;* so that it is enabled to feed upon the juices of a flower whose tubular corolla equals its trunk in length. Many animals whose mouths are adapted for suction, possess some means of attaching themselves to the spots in which they can best obtain the nutriment they require; thus we find the *Cystic* and *Cestoid Entozoa* very commonly provided with a set of hooklets on their heads; the *Trematoda* usually have the mouth surrounded by a circular sucker (Fig. 100, *a*); the *Suctorial Annelida* have not merely a sucker for attachment, but an incising apparatus for making incisions into the blood-vessels of the animals whose juices they suck; the *Suctorial Crustacea* usually have a sucker formed by the peculiar development of one of the pairs of members, whilst the mouth is elongated into a proboscis armed with penetrating instruments; and the *Suctorial Insects,* which seldom attach themselves permanently in any one situation, but make a fresh puncture whenever their appetite incites them to feed, are for the most part destitute of any special organs of adhesion, but have a most elaborate set of instruments for incising the skin of the animals they attack.—The *Cyclostome* Fishes (Fig. 146, A) are the only Vertebrated animals, which present any similar adaptation to a suctorial mode of nutrition.

144. When the food consists of solid matters, which is the case in by far the larger proportion of the Animal kingdom, we find the entrance to the digestive cavity of much greater proportionate size; and it is seldom prolonged forwards, but far more frequently has somewhat of a funnel shape, so that the aliment may be more readily drawn within it. The means by which the introduction of food is accomplished, are extremely various. The simplest plan is one which carries us back to the type of the Infusoria, although it presents itself in a much more elaborate form. Among many aquatic animals, whose food consists of minute particles diffused through the water, we find that the action of cilia, situated around and within the entrance of the alimentary canal, or upon organs in immediate connection with it, whereby a current of water may be driven into the stomach, is the sole means by which aliment is introduced. The most remarkable examples of entire dependence upon this agency are furnished by the Acephalous Mollusks; for in the *Bryozoa* (Fig. 49) the polype-like arms are unfitted for prehension, and effect the introduction of alimentary matter solely by the ciliary currents they produce; and the *Tunicata* (Fig. 42), *Brachiopoda* (§ 138), and *Lamellibranchiata* (Fig. 43), are all supplied with aliment in a manner essentially the same. Among Radiated animals, recourse seems less frequently had to this plan, which is obviously one that is unsuitable to those forms of the digestive cavity that have but a single orifice, since

the requisite current could not be effectually maintained through such; but among the *Ciliograde Acalephæ* (Fig. 101), which possess an anal orifice, the ciliary action appears to be the means of introducing aliment, as well as of propelling the body through the ocean. In the Articulated classes, too, this ciliary action is seldom the means of introducing aliment into the stomach; most of them feeding upon solid bodies of comparatively large dimensions, and being enabled by their locomotive powers to go in search of their food. But among those which resemble in their habits of life the Molluscous tribes already alluded-to, we find the same method of obtaining nutriment; thus it appears to be by the currents set in motion by the cilia clothing the respiratory tufts which are seated on their heads, that the *Serpulæ* and their allies (Fig. 144) draw in their food; and in the *Rotifera* (Fig. 96) and the *Cirrhipeda* (Fig. 4) we find special ciliated organs developed, which appear subservient both to the purposes of respiration and to the ingestion of aliment. It is probable that the *Amphioxus* (Fig. 127) is nourished in a similar manner; but that remarkable animal affords the only known example among the Vertebrata, of the employment of ciliary action for this purpose. It is curious to observe, however, in the Greenland Whale, a mode of ingestion which is essentially the same, though accomplished by a different instrumentality; for this huge animal gulps enormous volumes of water into its capacious mouth, and then ejects these through its blow-holes, straining out, through its whalebone-sieve, the small Medusæ, Pteropods, Crustacea, Fishes, or other free-swimming marine animals, which the water may contain; it being such alone that it is capable of swallowing.—The foregoing plan is one that seems intermediate, in regard to the kind of nutriment for which it is adapted, between the suctorial method, which is fitted only for the introduction of liquid aliment, and the one we have next to consider, which is appropriate to the ingestion of solid masses.

145. The organs with which the Digestive Apparatus is provided, for the introduction of *solid* food into its cavity, vary greatly in complexity in the different tribes of animals which derive their subsistence from aliment of this kind. Thus we shall find that in the lowest and simplest types, these organs are in immediate connection with the *stomach;* but that they are separated from it in the higher by the interposition of an *oral* apparatus, with prehensile appendages for laying hold of the food, which after passing through the buccal cavity, is drawn downwards into the stomach; and that in the highest of all, the introduction of food into the mouth is itself aided by accessory organs, which do not form part of its own organization. Of the first of these types, we have a characteristic example in the *Hydra* (Fig. 34), the entrance to whose stomach is surrounded by 'tentacula,' which may be considered as representing the pharyngeal and œsophageal muscles of higher animals. The tentacula of the *Actinia* (Fig. 35) correspond with these in character and in mode of

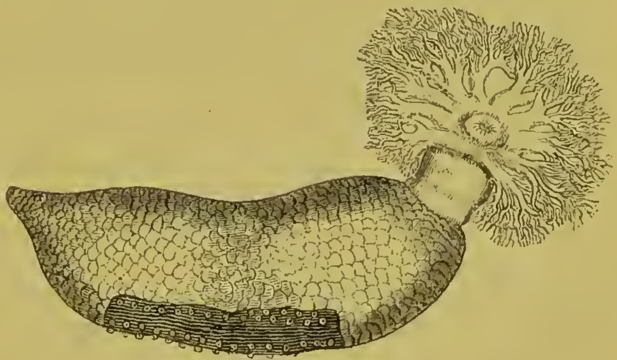
FIG. 93.



Thaumantias pilosella, one of the Naked-eyed Medusæ:—*a a*, oral tentacula; *b*, stomach; *c*, gastro-vascular canals, having the ovaries, *d d*, on either side, and terminating in the marginal canal *e e*.

action; and it may be said that the same type prevails through the whole class of Polypifera. The *Medusæ* and their allies are formed upon a plan which must be considered as essentially similar, the four tentacula (Fig. 93, *a a*) being there, also, placed around the entrance to the stomach; and it is by the adhesion of the edges of these tentacula, that the 'proboscis' is formed in such of the Pulmograde Acalephæ as possess it. It is interesting to observe in the class of *Echinodermata*, a gradual transition towards a more elevated type. Thus in the *Asterias* (Fig. 37), which has no oral apparatus, we find the food brought to the stomach, not by tentacula, but by the flexion of the lobes of the body, commonly known as their 'arms.' "Starfishes," says Prof E. Forbes,* "are not unfrequently found feeding on shell-fish; in such cases they enfold their prey within their arms, and seem to suck it out of its shell with their mouths pouting out the lobes of the stomach. They can project the central parts of their stomachs in the manner of a proboscis." Whether the true 'arms' of the *Crinoidea* (Figs. 9, 38) and of *Ophiurida* (Fig. 8), serve to bring food to the stomach, is not certainly known; but their position in the former of these orders, at least, would lead to the inference that they are subservient to this purpose. In the *Echinida* and *Holothurida*, however, we find that the entrance to the alimentary canal is no longer the entrance to the stomach; but that the former becomes a true 'mouth,' being furnished with a prehensile apparatus of its own, and being separated from the stomach by the intervention of the œsophagus. The mouth is provided, in the typical Echinida, with a dental apparatus (Fig. 95, *a*), which is capable of being projected beyond the oral orifice; whilst in the Holothurida (Fig. 94), it is surrounded by prehensile tentacula, which are here to be regarded as *labial*, being extensions of the lips, rather than as a divided pharynx.—Turning to the Articulated series, we find that in a considerable proportion of the *Annelida*, the mouth is furnished with powerful jaws, sometimes to the number of three pairs, opening laterally; or with a proboscis which is capable of being everted, and which then displays an armature of teeth on its exterior (Fig. 53, B, C). In the *Mandibulate Insects*, and in the greater part of the *Crustacean* class, we find the jaws highly developed, and taking the place of any other kind of apparatus; the former group always possessing two pairs of these organs, which open laterally, one above and the other below the oral orifice; whilst in the latter, besides the regular mandibles and maxillæ, there is a variable number of feet-jaws (§ 53).—In the higher part of the Molluscous series, again, the mouth is usually provided with

Fig. 94.



Holothuria phantapus.

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* "History of British Echinodermata," p. 86.

jaws; these animals being adapted to go in search of their food, and to select and divide it for themselves. In many of the *Gasteropoda*, we find a single pair of horny jaws, opening laterally; but there are several whose buccal apparatus rather consists of a proboscis-like organ, somewhat resembling that of the Annelida, which can be everted, and which then displays a set of powerful teeth, adapted to abrade substances of even shelly hardness. The *Cephalopoda*, on the other hand, possess a pair of horny jaws opening vertically, like those of Vertebrata.—Throughout the Vertebrated series, it is almost invariably by the action of the jaws and lips, that food is introduced into the mouth; the suctorial *Cyclostomi* already referred-to, and the *Syngnathidæ* or 'pipe-fishes,' which have the jaws prolonged and adherent together, and which seem to draw up worms, small mollusks, and crustaceans, and the ova of other fishes, through the tube thus formed, being the only cases of even partial reversion to the lower type.

146. *Prehensile Appendages.*—Among the more elevated forms of the Molluscous, Articulated, and Vertebrated sub-kingdoms, we find a special provision for the *prehension* of food, by organs which have no immediate connection with the digestive apparatus; the aliment being thus brought within reach of the mouth and of its proper appendages. Some approaches to such an arrangement present themselves even in the lower Echinodermata, in which the 'arms' and lobes of the body are made to bring the food to the entrance of the stomach; and in the *Echinida* it seems not improbable that the spines and 'cirrhi,' especially the latter, may be occasionally used in subservience to the ingestion of food, as well as in locomotion.—Of the higher or Cephalous group of Mollusca, we only find the Cephalopoda and a few of the Pteropoda to be provided with prehensile appendages. The little *Clio* (Fig. 46, c) has three tentacula on each side of the oral orifice, beset with an immense multitude (estimated at about 60,000 on each) of minute suckers; and these seem to prefigure the 'arms.' Of such 'arms,' the *Nautilus* and its allies possess about a hundred; but being short and unfurnished with suckers, they are not nearly so efficient as instruments of prehension, as are the eight or ten acetabulated arms of the Sepia and its allies (Fig. 47). These arms, although resembling the tentacula of the Polypes* in uses, and apparently also in position, are not really homologous with them (§ 41); nor are they represented (as has been supposed) by the *labial* tentacula which are possessed by several Fishes, as well as by many of the inferior Mollusks.—In most of those higher *Articulata* which possess numerous well-developed members, we find that such as are nearest the mouth are used to a greater or less extent in the prehension of food; and that in many instances one pair is specially developed for this purpose. The transition from the general to the special form of the prehensile apparatus is well seen among the *Decapod Crustacea* (§ 52); in some of which (as the Cray-fish) we find all the true legs of nearly equal size, and most of them terminated by forcipated appendages; whilst in others (as the Crab) the first pair are enormously developed as prehensile organs, and are furnished with powerful pincers, whilst the remainder are restricted

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* The 'Polype' of the ancients was the Eight-armed Cuttle-fish of the Mediterranean; and it was from their superficial resemblance to this creature, that the designation was applied to the beings now known as Polypes, when their Animal nature was first made out.

to locomotive action.—In the *Vertebrated* series, it would appear as if the limited number of members, and the necessity for employing these in locomotion, placed a greater restriction upon the use of them as prehensile organs. Among Fishes and Reptiles, the prehension of food is solely accomplished by the jaws, save where the tongue (as in the Chameleon) is subservient to this function. In Birds, it is only in a few cases that the foot is employed for this purpose, the anterior members being never modified in subserviency to it, and the tongue (as in Reptiles) being the only instrument that is ever specially developed as a prehensile organ. Among Mammals, the special modification of the anterior extremities for prehension is limited to those few groups in which they are comparatively little needed for locomotion: thus, among most of the Unguiated quadrupeds which have the power of standing erect upon the hind legs, as the Rodentia, Plantigrade Carnivora, and many Marsupialia, we find the anterior extremities employed to clasp objects between them; in the Quadrumana, the prehensile power is exercised by a single extremity, which can hold an object of moderate size in the grasp of the digits; but it is in Man that this prehensile power is carried to its fullest extent, by the peculiarity of conformation of the thumb, which brings its extremity into opposition with those of each of the fingers.—Some of the Mammalia whose extremities are not adapted for the prehension of food, are furnished with other organs for the purpose, which are special modifications of those elsewhere existing under the ordinary type; it is sufficient to refer to the proboscis of the Elephant, the prolonged snout of the Tapir, the prehensile tongue of the Giraffe, and the very extensible tongue of the Ant-eater.

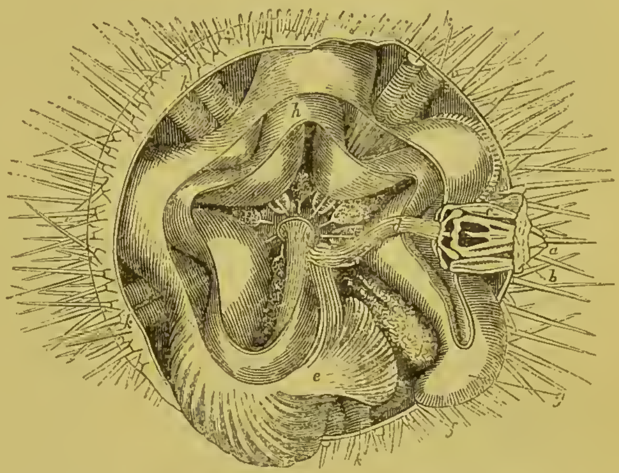
147. Thus, between the simple stomach furnished with prehensile tentacles, of which the *Hydra* consists, and the complex apparatus for the prehension of the food which is placed in front (so to speak) of the cardiac orifice of the stomach in *Man*, a regular gradation may be traced. The tentacula are brought together, to form a pharyngeal tube; a buccal cavity is placed at its entrance; jaws and lips are developed at the orifice of the buccal cavity; and external members are developed or modified, for the purpose of bringing the food within their reach. Yet the development of these more special organs does not supersede the necessity of those more generally diffused through the Animal kingdom. Although the hand of Man brings his food *to* his mouth, yet it is by his lips and jaws that his food is taken *into* its cavity, as in the Herbivorous Mammalia; and notwithstanding that the muscular apparatus of the mouth propels the food backwards into the pharynx, it only thereby carries it within reach of the pharyngeal constrictors, which then lay hold of it and draw it into the œsophagus, by the muscles of which it is carried down into the stomach, precisely as by the tentacula in the *Hydra*. And it is curious to observe, that just as the tentacula of the Hydra no longer make any attempts to grasp an object that touches them, when the stomach is already gorged with food, so does Man experience a difficulty in the act of swallowing at the end of a full meal, which seems to result from a like want of readiness to contract on the part of the pharyngeal constrictors.—In the progress of the food along the alimentary canal of higher Animals, we may observe the gradual removal of it from connection with the functions of *animal* life. To procure it in the first instance, is one important office of these functions; and the highest exercise of the

locomotive, sensorial, and intellectual powers is often required for this purpose. Its introduction into the mouth is an act of volition in Man; whilst the masticatory movements to which it is there subjected, may be regarded as essentially 'automatic' in their character (though capable of being controlled and directed by the will), and as closely corresponding with the instinctive actions of the lower animals. The act of 'deglutition,' or swallowing, is of a purely 'reflex' nature, being the result of a nervous influence in which neither the will nor sensation is concerned; for when the solid or fluid contents of the mouth are brought in contact with the surface of the pharynx, the impression made upon the nerve distributed on it is transmitted to the upper part of the spinal cord; and an automatic impulse is propagated along the motor fibrils, by which the muscular movements requisite for the action of swallowing are produced. A similar action assists the propulsion of food down the œsophagus, and the movements of the stomach seem to be in part excited in the same manner; but the proper fibres of the œsophagus itself are *not dependent* for their power of action upon nervous influence, nor are those of the stomach. Beyond the stomach, the connection of the motions of the alimentary canal with the nervous system almost wholly ceases, the ordinary peristaltic movements of the intestines appearing to depend upon the stimulus directly applied to their muscular coat by the contact of food; although they may be in some degree controlled by a system of muscles disposed around the outlet of the canal, which are, like those at its entrance, partly involuntary, and partly under the direction and restraint of the will.—So, in descending the Animal scale, we find that the introduction of food into the digestive cavity is first removed from the agency of the intellect and will, and provided-for by the instincts alone; this is probably the case in even the highest Invertebrata, and likewise in the lower Vertebrata, as it undoubtedly is in the infantile condition of Man. When we descend to Zoophytes, we find strong reason to believe that the movements of the tentacula, by which the food is grasped and drawn into the stomach, are not merely involuntary, but are not even dependent upon sensation; and there is still stronger reason to believe that such is the case, in those inferior Mollusks in which the supply of food is obtained by ciliary currents. And thus we may perceive a regular gradation between those beings, in which the supply of food has been made (for a wise purpose) dependent upon the highest exercise of the functions of *Animal* life, and those in which the operation is as purely *Organic* as it is in Plants. (See CHAP. XIII.)

148. *Reducing Apparatus.*—One more class of accessory organs has to be noticed, before we proceed to the account of the essential part of the Digestive apparatus, and of the operations to which it is subservient. In order that solid food may be more easily dissolved in the stomach, it is frequently submitted in the first instance to a process of mechanical reduction by a triturating apparatus; and either at the same time, or at some other, it is incorporated with a Salivary fluid, the admixture of which not only renders the subsequent process of solution more easy, but also appears to effect a change in the alimentary matters themselves. It is in animals that are destined to feed upon vegetable substances, and especially upon such as are of tough consistence, that we find this reducing apparatus most powerful and efficient; for as the flesh of animals is

of comparatively easy solubility, there is less occasion for any such preliminary preparation. This reduction is not by any means constantly performed, however, in the mouth; for almost any part of the first division of the alimentary canal may be the seat of the apparatus.—In the Radiated sub-kingdom, there are none save the typical *Echinida*, which possess such a reducing apparatus; but it is remarkable that it should attain in that group an extraordinary complexity, and should occupy a situation corresponding to that which it possesses in the highest Vertebrata. The 'lantern of Aristotle' (Fig. 95, *a*), as it is sometimes termed, is a five-sided conical mass, composed of five 'jaws' in apposition with one another, each of them having the form of a triangular pyramid; two of their sides, which are flattened, look towards those of the neighbouring jaws, and have their surfaces roughened by grooves like those of a file; whilst the third, which is somewhat convex, is external, and serves for the attachment of the muscles that fix the apparatus to the interior of the shell, which is furnished with projections round the oral orifice developed for this purpose. Each jaw contains a long pointed tooth of remarkable hardness, which projects to a considerable length from its socket, and this appears (like the 'tusks' of Mammalia) to be continually renewed by new growth at its base, as it is worn away at its apex. The whole is moved by a most complete set of muscles, which can bring the entire 'lantern' nearer to the oral orifice, and can cause the points of the teeth to project beyond it; which can separate the jaws, and consequently the points of the teeth, from one another, and then draw them together, so as to enable the latter to grasp and divide any hard substance adapted for food; and which can subject this to trituration, not merely between the points of the teeth, but also between the flattened file-like surfaces of the jaws, which can be made to work against each other.—Among the Acephalous Mollusks, no reducing apparatus seems usually to be required; their food being in a state of very fine division at the time it is introduced; nevertheless in some of the *Bryozoa*, a 'gizzard' or muscular stomach, apparently subservient to this purpose, intervenes between the œsophagus and the true digestive stomach. A gizzard of considerable power, closely resembling that of Birds, is found in many Gasteropods, especially in those whose mouth is unfurnished with a reducing appa-

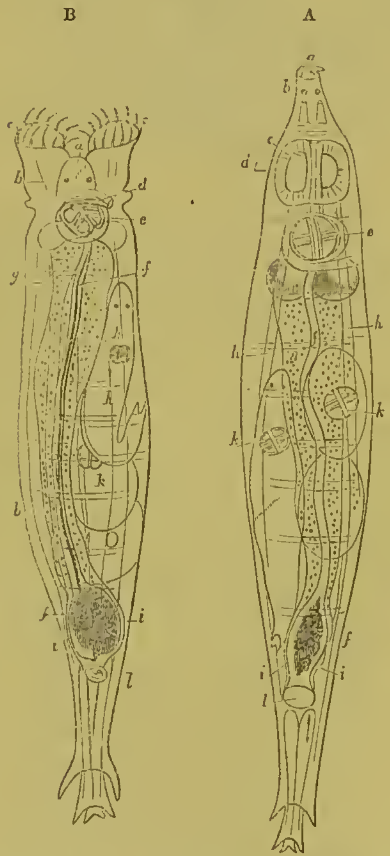
Fig. 95.



Anatomy of *Echinus lividus*, laid open, from the under side;—*a*, buccal apparatus turned to one side; *b*, portion of tegumentary membrane surrounding the mouth; *c*, calcareous jaws; *d*, œsophagus; *e*, commencement of intestine; *f*, mesenteric membrane; *g*, duplicature of the intestine, which forms a second convolution, *h*, along the course of the first, and terminates at the anal orifice *i*, around which are seen the five oviducts; *j*, ovaria; *k k*, ambulacral vesicles.

ratus; this is the case, for example, with *Aplysia* (Fig. 50), whose gizzard (*i*), situated between the crop (*g*, *g*) and the true digestive stomach (*h*), is lined with firm horny teeth; and in some instances, these teeth are replaced by firm calcareous plates, adapted to crush the shells of the smaller Mollusks that are devoured by these animals, which is the case in *Bulla*.* But in the greater number of instances, the reduction of the food is accomplished by some part of the buccal apparatus; either by the cutting jaws with which some Gasteropods are furnished; or, as in *Buccinum*, by the teeth which form a sort of palatal lining to the proboscis, and which are carried outwards by its eversion; or, as in *Patella* and some other phytophagous Gasteropods, by the long rasp-like tongue. In the *Cephalopoda*, notwithstanding the presence of jaws for the division of the food, its reduction seems to be chiefly accomplished by a muscular gizzard closely resembling that of Birds.—In most of these instances, we find salivary glands pouring their secretion into the mouth or pharynx; and where a gizzard exists, there is usually also a 'crop' or 'first stomach' (which is rather to be regarded as a dilatation of the lower part of the œsophagus), into which the food is received in the first instance, and in which it is probably macerated in the salivary fluid before being subjected to the trituration of the gizzard.

Fig. 96.



Rotifer vulgaris, as seen at A with the wheels drawn-in, and at B with the wheels expanded:—*a*, mouth; *b*, eye-spots; *c*, wheels; *d*, siphon; *e*, jaws and teeth; *f*, alimentary canal; *g*, glandular(?) mass inclosing it; *h*, longitudinal muscles; *i*, *i*, tubes of water-vascular system; *k*, young animal; *l*, cloaca.

149. In the lower Articulata, there is seldom any special reducing apparatus; in the *Rotifera*, however, which obtain their food (like the Bryozoa) by ciliary action, we find, in place of a gizzard, a curious pair of jaws (Fig. 96, *e*), furnished with sharp hard teeth, and worked by a complex muscular apparatus; these are situated in the pharynx, and serve to divide the larger particles as they pass downwards to the stomach. Owing to the transparency of these animals, the movements of their jaws can be distinctly seen, when the 'wheels' are in action, and are driving downwards the particles which have entered the mouth.—In the *Mandibulate Insects*, the reduction of the food, as well as its division and ingestion, is partly performed by the jaws, and the mouth is usually furnished with salivary glands; but many insects are also provided with a gizzard, which, as in the cases already alluded-to, does

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* The Author once met with an entire shell of *Pandora rostrata* in the gizzard of a Bulla.

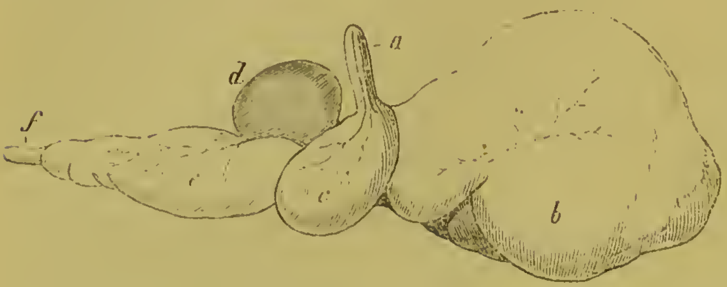
not act upon the food until it has been received into the crop. In many of the higher *Crustacea*, notwithstanding their complex buccal apparatus, the stomach is furnished with a powerful set of teeth, affixed to a complicated framework which is worked by powerful muscles, so as to constitute very efficient reducing instruments. Among the mandibulate Articulata, salivary glands are almost invariably found opening either into the mouth, pharynx, or œsophagus; but sometimes the stomach itself is clothed with cæca, that appear to have a similar character.—Of that dental reducing apparatus, which is so especially characteristic of the Vertebrata, some notice has already been taken (§§ 60, 64, 72); it may, however, be here remarked that the bones surrounding the mouth are far more copiously set with teeth in Fishes, than they are in the higher animals, for there is scarcely any one of these bones that is not furnished with them in some tribe or other, and they sometimes all bear them at once; among Reptiles they present themselves on the palatine and pterygoid bones and the vomer, though they are limited to the jaws in Sauria; and with the higher specialization which the dental apparatus acquires in Mammals, we find it always restricted to the jaws alone. In the class of *Birds*, the deficiency of teeth is supplied by an adaptation of the stomach for mechanical reduction, that carries us back to the plan so common among the Invertebrata. There is this curious distinction, however, that the gizzard succeeds, instead of preceding, the proper gastric cavity (Fig. 105, *d*); the food being not only entirely macerated in the salivary and other secretions furnished by the crop, but also impregnated with the proper gastric fluid, before it is subjected to the triturating action of the gizzard.

107 d

150. Although in the *Mammalia* the reducing apparatus is limited to the mouth, yet the stomach frequently presents a complex arrangement, of which the purpose seems to be to favour the mechanical reduction of the food, and its impregnation with fluid, before it is subjected to the true digestive process. The most remarkable example of this kind is presented in the group of *Ruminantia*, in which the stomach is subdivided into four distinct cavities; the first two of these, however, being rather dilatations of the œsophagus, than parts of the stomach itself. The solid food, on its first passage down the œsophagus in a crude unmasticated state, enters the large cavity termed the *ingluvies* or 'paunch' (Fig. 97, *b*), which, like the crop of Birds, serves as a temporary receptacle for it, and moistens it with the fluid secreted from its walls; the liquid swallowed, on the other hand, seems to be specially directed into the second cavity (*c*), which is termed the *reticulum* or 'honeycomb-stomach' from the reticulated appearance of its interior, occasioned by the irregular folding of its internal membrane. It is here that the peculiar provision of 'water-cells' is found, for which the Camel has long been so celebrated, but which exists in a greater or less degree in all the Ruminants. These cells, which are the spaces between the deepest reticulations, are bounded by muscular fasciculi; by the contraction of one set of which their orifices may be closed and their contents retained; whilst by that of another set, the fluid they contain may be expelled into the general cavity of the stomach. After remaining there until sufficiently impregnated with fluid, the solid matters which have passed into the first and second stomachs are returned at intervals, in the form of little balls or pellets, to the mouth; where they undergo a

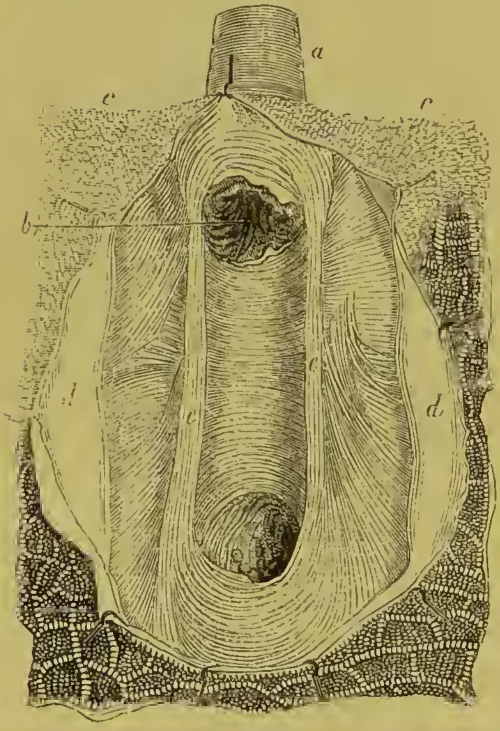
thorough mastication, and are completely incorporated with salivary fluid. When finally swallowed, the food is directed, in the manner to be presently described, into the third stomach (*d*), the *omasum*, commonly called the 'many-plies' from the peculiar manner in which its lining membrane is disposed; this presents a number of folds, lying nearly close to each other like the leaves of a book, but all directed by their free edges to the centre of the tube, a narrow fold intervening between each pair of broad ones. The food, now reduced to a pulpy state, has therefore to pass over a large surface, before it can reach the outlet of that cavity; which leads to the *abomasum* or fourth stomach (*e*). commonly called the *reed*. This is the seat of the true process of digestion, the gastric fluid being secreted from it alone; and it is from this part of the calf's stomach that the 'rennet' is taken, which derives its extraordinary power of coagulating milk from the organic acid it contains. In the sucking animal, the milk which forms its nourishment passes directly into this stomach; the aperture leading to the first and second being closed, and the folds of the third adhering together so as to form a narrow undivided tube. — The direction of the food into one or another of these cavities appears to be effected without any voluntary effort on the part of the animal itself, but to result simply from the very peculiar endowments of the lower part of the œsophagus. This does not entirely terminate at its opening into the first stomach or paunch, but it is

Fig. 97.



Stomach of *Sheep*;—*a*, œsophagus; *b*, ingluvies, or paunch; *c*, reticulum, or honeycomb-stomach; *d*, omasum, or many-plies; *e*, abomasum, or reed; *f*, pylorus.

Fig. 98.



Section of part of the Stomach of the *Sheep*, to show the demi-canal of the œsophagus; the mucous membrane is for the most part removed, to show the arrangement of the muscular fibres.—At *a* is seen the termination of the œsophageal tube, the cut edge of whose mucous membrane is shown at *b*. The lining of the first stomach is shown at *c, c*; and the mucous membrane of the second stomach is seen to be raised from the subjacent fibres at *d*. At *e, e*, the lips of the demi-canal are seen bounding the groove, at the lower end of which is the entrance to the third stomach or many-plies.

continued onwards as a deep groove with two lips (Fig. 98): by the closure of these lips (*e, e*) it is made to form a tube, which serves to convey the food onwards into the third stomach; but when they separate, the food is allowed to pass either into the first or the second stomach. When the food is first swallowed, it has undergone but very little mastication; it is consequently firm in its consistence, and is brought down to the termination of the œsophagus in dry bulky masses. These separate the lips of the groove or demi-canal, and pass into the first and second stomachs. After they have been macerated in the fluids of these cavities, they are returned to the mouth by a reverse peristaltic action of the œsophagus; this return takes place in a very regular manner, the food being shaped into globular pellets by compression within a sort of mould formed by the ends of the demi-canal, drawn together, and the pellets being conveyed to the mouth at regular intervals, apparently by a rhythmical movement of the œsophagus. After its second mastication, it is again swallowed in a pulpy semi-fluid state; and it now passes along the groove which forms the continuation of the œsophagus, without opening its lips; and is thus conveyed into the third stomach, whence it passes to the fourth. Now that the condition of the food as to bulk and solidity, is the circumstance which determines the opening or closure of the lips of the groove, and which consequently regulates its passage into the first and second stomachs, or into the third and fourth, appears from the experiments of Flourens;* who found that when the food, the first time of being swallowed, was artificially reduced to a soft and pulpy condition, it passed for the most part along the demi-canal into the third stomach, as if it had been 'ruminated,'—only a small portion finding its way into the first and second stomachs.

151. *Digestive Apparatus.*—We have now to trace-out the principal forms under which the proper Digestive apparatus presents itself in the different classes of animals; and the mode in which it operates. Putting aside that of the *Protozoa*, which has been already considered (§ 139), the simplest of all its conditions is that under which we find it in the *Hydra*, *Actinia*, and other solitary Zoophytes. Thus in the *Hydra* (§ 38), it will be remembered, the stomach occupies the whole of the cavity enclosed by the outer walls; and the membrane with which it is lined is so completely identical with that which forms the external integument, that the one may be made to take the place of the other without any injury to the animal. Yet it is obvious that a powerfully-solvent fluid is secreted from the walls of the gastric cavity; for the soft parts of the food which is drawn into it (usually in a living state) are gradually dissolved, and this without the assistance of any mechanical trituration; whilst the hard parts are ejected again by the orifice through which they were introduced. The product of this operation appears to be absorbed from the lining of the digestive sac, by the whole of the tissue which surrounds it; and to be conveyed into the tentacula (which are the only parts not in immediate relation with the digestive cavity) by interstitial lacunæ left for that purpose.—In the compound *Hydroida*, on the other hand, the lower part of the digestive sac of each polype is prolonged into a tube, which communicates with similar prolongations from other polypes,

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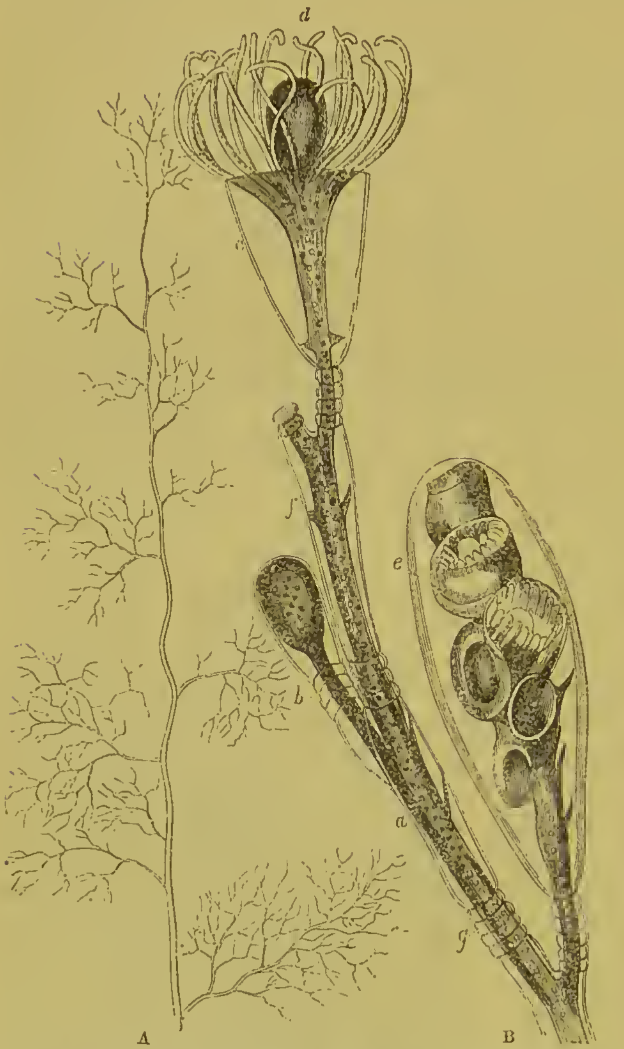
* "Ann. des Sci. Nat." (1832), Tom. xxviii; and "Mémoires de Physiologie Comparée," 1843.

so that the stem and branches of the entire arborescent structure contain a continuation of the gastric cavities of the several polypes which they bear (Fig. 99); and the fluid that has been prepared by the digestive operations of the latter, passes through the aperture at the lower extremity of each (which is guarded by a sphincter muscle), and is received into the system of ramifying tubes, which may be considered as an extension of the digestive cavity throughout the general structure, for the purpose of conveying to every portion of it, and especially to such parts as are undergoing increase by the formation of new branches or polype-cells, the materials prepared for nutrition. Through this system of canals, the contained fluid has been observed to move with considerable regularity, and in a manner that cannot be accounted-for by any mechanical agency communicated by the contraction of the stomachs of the polypes. Thus, when the stem and branches of a living *Sertularia* are examined with a sufficiently high magnifying power, a current of granular particles is seen moving along the axis; which, after continuing one or two minutes in the same direction, changes and sets in the opposite one, in which it continues about as long, and then resumes the first; thus alternately flowing down the stem to the extremities of the branches, and back again. The change of direction is sometimes immediate; but at other times the particles are quiet for a while, or exhibit a confused whirling motion for a few seconds, before it takes place. The current extends into the stomachs of the polypes; in which, as well as in their orifices, a continual agitation of particles is perceptible.

Fig. 99.



Campanularia gelatinosa; A, upper part of the stem and branches, of the natural size:—B, a small portion enlarged, showing the structure of the animal;—*a*, terminal branch bearing polypes; *b*, polype-bud partially developed; *c*, horny cell, containing the expanded polype *d*; *e*, ovarian capsule, containing medusiform gemmæ in various stages of development; *f*, fleshy substance extending through the stem and branches, and connecting the different polype-cells and ovarian capsules; *g*, annular constrictions at the base of the branches.

When these particles are allowed to escape from a cut branch, they exhibit for a time an apparently spontaneous motion. No contraction of the tube, any more than of the stomach, seems concerned in the production of the currents; and their rapidity and constancy appear intimately connected with the activity of the nutritive processes taking place in the parts towards which they are directed, the predominant 'set' of the current being *towards* any portion which is undergoing development, and *away from* any part which exhibits a diminution or loss of vitality. In the *Tubularia*, in which the polype-bearing stem ramifies but little, or not at all, and is sometimes divided by nodes or partitions somewhat resembling those of the *Chara* (CHAP. VIII.), the movement of fluid very strongly resembles that which is seen in that plant; for the current passes down one side, crosses the septum, and then ascends the other side, following a somewhat spiral line of particles deposited on the walls of the tube.*

152. The condition of the digestive apparatus in the *Actiniform* and *Alcyonian* Zoophytes, does not essentially differ from that just described; save in the fact that the stomachal sac does not occupy more than the central portion of the body, being surrounded by a visceral cavity which is subdivided by radiating partitions into chambers containing the generative apparatus. With this visceral cavity the stomach communicates, alike in the Actinia† and in the Alcyonium, by a circular orifice at its base (Fig. 100, *d*), which is surrounded by a muscular sphincter; and thus the fluid product of digestion, together with water introduced for the purpose of respiration, can pass freely from the stomach into the surrounding chambers, and into the cavities of the tentacula. In most species of Actinia (if not in all), the tentacula have pores at their extremities; and the broad leaf-like tentacula of the Alcyonia have pores in the papillæ which fringe them. These pores can scarcely be regarded in the light of anal orifices, the indigestible parts of the food swallowed by these animals (such as the shells of crabs and mollusks) being rejected by the mouth.—In the composite *Helianthoid* Zoophytes, the several polypes, whilst framed on the same general plan with the Actinia, communicate with each other more or less freely by orifices and passages between their respective visceral cavities. In the *Zoanthidæ*, whose polypes are comparatively isolated, this communication is established by a stalk-like prolongation from the base of each, almost as in the compound Hydroida. But in the compound *Fungiæ*, *Astreæ*, *Meandrinæ*, and other Zoophytes, whose associated polypes encase stony lamelliform corals, the connection is formed by numerous lateral openings: and where the polypes are separated by intervening fleshy tissue, these openings form a system of passages through it, which must be regarded as continuations of the visceral cavities of the Polypes themselves. So intimate in many

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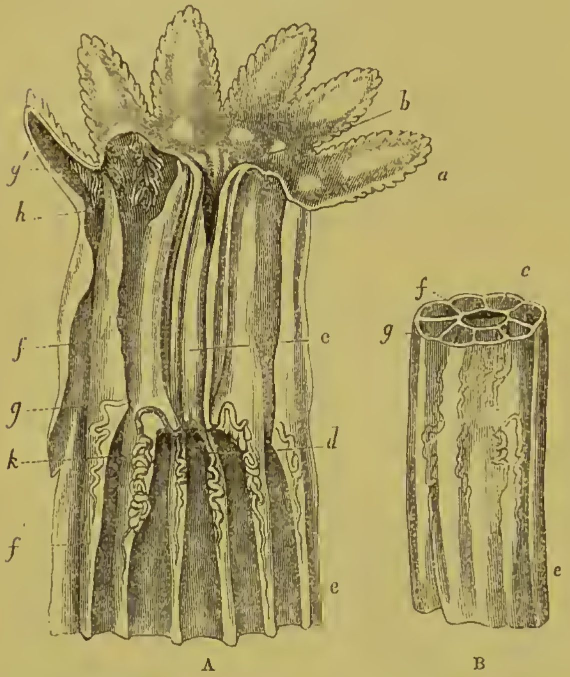
* See the Memoir of Mr. Lister 'On the Structure and Functions of Tubular and Cellular Polypi,' in "Philos. Transact.," 1834; and that of Prof. Allman 'On Cordylophora lacustris,' in "Philos. Transact.," 1853.

† In the previous editions of this work, it was inadvertently stated that the stomach in the Actiniais closed at the bottom. All recent investigators, however, agree in affirming that a definite communication exists between the stomach and the visceral cavity, though the orifice is frequently of small size. The earliest description of this structure which the Author has met with, is contained in Mr. Teale's 'Observations on the Anatomy of Actinia Coriacea,' in the "Trans. of the Leeds Philos. Soc.," Vol. I., 1836.

instances is the connection thus formed, that the "adjacent polypes have scarcely anything but a mouth that can be said to be private property."* Hence the transition is easy to the Alcyonian or *Asteroid* Zoophytes, among which the general cavity of the body (Fig. 100, *e*), into which the stomach of each Polype opens at its base, communicates so freely with that of other polypes of the same polypidom, that the whole assemblage forms a system of canals extending through the mass, very much after the manner of those of a sponge.—This kind of communication results, in all the foregoing cases, from the extension of the fabric by gemmation; the visceral cavity of each newly formed part being an offset from that of a previously existing polype; and the connection, which is at first extremely free, being never entirely closed.

Fig. 100.



Terminal portion of *Alcyonian* polype, considerably enlarged, and laid open (A) longitudinally, (B) transversely, to show the interior structure;—*a*, tentacula; *b*, mouth; *c*, stomach; *d*, its inferior opening into the general cavity, of which the upper part is seen at *e*; *f*, longitudinal partitions traversing the space between the stomach and the external parietes; *f'*, prolongations of these, as folds in the wall of the general cavity; *g*, canals surrounding the stomach, and communicating with the cavity of the tentacula; *g'*, one of the tentacula laid open; *h*, groups of spicules situated at the base of the tentacula; *k*, filiform appendices.

153. The conformation of the digestive apparatus among the *Acalephæ* does not present any decided advance upon the Zoophytic type. In the lower 'composite' forms of this group, the plan of structure is essentially the same as in the Compound Hydroida; the stomachal cavities of the several polypoid bodies being in free communication with each other. In the *Medusæ* and their allies, however, we find an arrangement which more reminds us of the Actiniform type. From the central stomach, which is generally imbedded in the substance of the disk, but sometimes hangs down from its highest point like a pedicle, a set of radiating canals pass off towards the edge of the disk, where they usually communicate with a marginal vessel. The simplest arrangement of these 'gastro-vascular canals' is seen in the 'naked-eyed' Medusæ (Fig. 93), in which they are usually only four in number, and never anastomose with each other. In the 'hooded-eyed' Medusæ, the radiating canals are more numerous at their central commencement, and their number is further greatly increased by subdivision towards the margin of the disk (Fig. 36);

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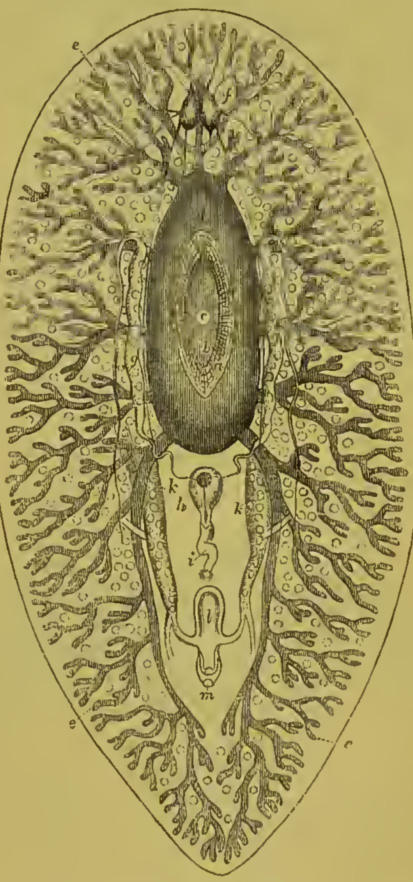
* See Dana "On the Structure and Classification of Zoophytes," Philadelphia, 1846; pp. 45—48.

frequently, too, they anastomose with each other, especially in their peripheral portion; and sometimes the anastomosis is so free, that this system of prolongations from the stomach forms a complete vascular network near the margin of the disk (Fig. 92).—A series of apertures communicating between the marginal vessel and the external surface, has been described by Prof. Ehrenberg in *Cyanœa aurita* (Fig. 36, *e*, *e*); but the existence of these is doubtful. Should they be really present, they would not be more entitled to be regarded as 'anal pores,' than are the orifices of the tentacula of Actiniæ. In fact, the gastro-vascular system of Medusæ may be likened to the radiating chambers into which the visceral cavity of Actiniæ is subdivided; the chief difference being, that its cavities are lengthened-out in accordance with the expansion of the disk. There are links of connection, in fact, which establish the transition from one form to the other.

154. The same type is exhibited under a higher form and more complete development, in the Digestive apparatus of some of those more elevated members of the Radiated series, which constitute the class *Echinodermata*. In the *Ophiurida* (Fig. 8) and *Asteriada* (Fig. 37), the gastric cavity is still a single sac, occupying the centre of the body, and furnished with but one orifice, through which food is drawn in, and indigestible or fæcal matter is ejected. But the sac is now completely cut off from the general cavity of the body, in which it is freely suspended. In the cæcal prolongations of the central stomach of the Asterias, and in the abundance of the cells which line them, we find the first manifestation of special glandular organs for the elaboration of the fluids required in the digestive processes, though the precise nature of these is as yet unknown. The proper digestive apparatus appears to be limited in the Star-fish, as in the Ophiura, to the *central* cavity; and being removed by a considerable interval from other parts of the body, it does not here directly convey the nutritious food to the tissues which make use of it; and the intervention of a set of vessels becomes requisite, for its absorption and transmission to distant parts.—The peculiar manner in which the lowest members of the Ar-

Fig. 101.

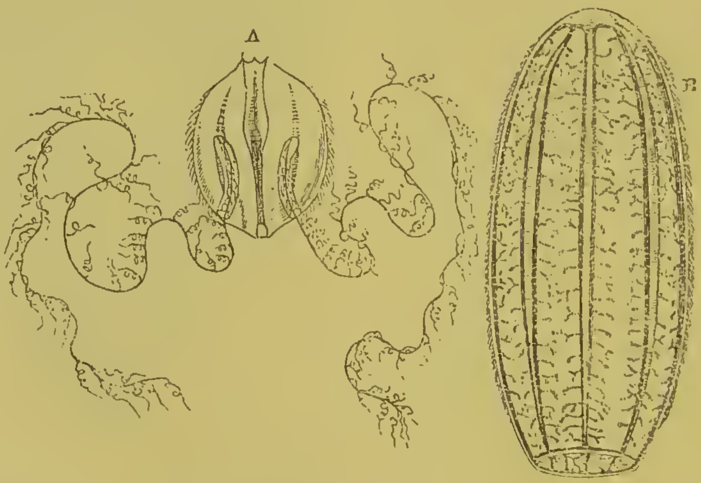


Structure of *Polycelis levigatus* (one of the Planariæ):—*a*, mouth, surrounded by its circular sucker; *b*, buccal cavity; *c*, œsophageal orifice; *d*, stomach; *e*, ramifications of gastric canals; *f*, cephalic ganglia and their nervous filaments; *g*, *g*, testes; *h*, vesicula seminalis; *i*, male genital canal; *k*, *k*, oviducts; *l*, dilatation at their point of junction; *m*, female genital orifice.

ticulated series, constituting the *Cestoid* tribe of Entozoa, obtain their nutriment, renders it unnecessary, as already remarked (§ 138), that they should be furnished with a digestive cavity; and in the higher group of *Trematoda*, as also in the tribe of *Planariæ*, which (if not actually included within it) is closely allied to it, we still find the stomach furnished with but a single orifice (Fig. 101, *a*), which must serve equally as mouth and anus. It is a remarkable feature in the structure of these animals, that from their principal stomach (*d*), a series of ramifying cæca are prolonged through the whole substance of the body. These do not lie loosely in a visceral cavity, but seem channelled out, as it were, in the midst of solid parenchyma; but it is affirmed by Quatrefages that a visceral cavity really exists, and that the digestive sac is tied to its walls by bands and filaments interlacing in every direction, so as to form a kind of areolar tissue that fills up the intervening space.—On nearly the same grade with the preceding, as regards the conformation of its digestive apparatus, we may place the curious *Rotiferous* Animalcule, of which the male has been already noticed as entirely agastric (§ 137): for the female possesses neither intestine nor anal orifice, and must eject the indigestible particles of food through its mouth. These are the only known instances among the Articulata, in which the digestive cavity has but one orifice.—No conformation of a similar kind is ever met-with, either in the Molluscous or in the Vertebrated series.

155. We have now to glance at those higher forms of the digestive apparatus, in which a second orifice or ‘anus’ is present, for the discharge of indigestible or fæcal matters; and this, as we shall see, is by far the most general plan of conformation. Although this orifice may externally be situated in the neighbourhood of the mouth, yet it always communicates with the part of the digestive cavity that is most remote from it; this cavity being usually more or less prolonged in the form of a tube.

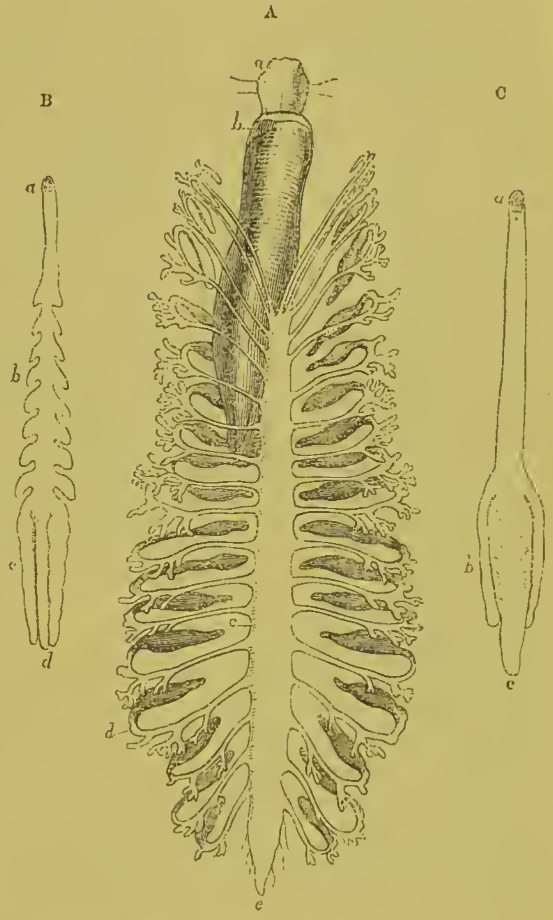
Fig. 102.



A, *Cydippe pileus.*—B, *Beroe Forskalii*, showing the tubular prolongations of the stomach.

The lowest animals which present this great advance in the type of conformation, are the *Ciliograde Acalephæ* (Fig. 102), which in this important particular differ widely from the rest of their class, so that some Zoologists remove them from it altogether. As in the Medusæ, we find the deficiency of blood-vessels supplied by tubular prolongations of the gastric cavity (B), which extend themselves into the substance of the tissues, and which convey to them the materials for their growth and renovation. In the *Cydippe* (A) we see the first indication of that division between the 'stomach' and 'intestinal canal,' which becomes so much more obvious and important in the higher classes. This division is by no means well marked, however, even in the highest Radiata; the alimentary canal, which commences with the mouth and terminates at the anus, being of nearly uniform size throughout, and apparently of similar endowments; as we see in the *Echinus* (Fig. 95), and the *Holothuria* (Fig. 40.) In the *Nematoid* Entozoa, again, the same uniformity presents itself (Fig. 52); and it is curious to observe this almost exactly repeated in the *Serpent* tribe, whose organisation is so much higher; but the prolongation and uniformity of whose body seems to necessitate a somewhat similar conformation of the alimentary canal. Even in the *Annelida*, the same general plan is continued with but little modification; the alimentary canal passing in a straight line from one extremity to the other, without distinction of stomach or intestine (Fig. 103); but from its sides we find cæcal prolongations extending, sometimes as a single pair of prolonged tubes (C, *b*), sometimes as mere sacculi in the walls of the stomach (B, *b*), and sometimes as a multiplied and extended series of appendages (A, *d*), which seem, like the radiating cæca of the Asterias, to be rather glandular in their character, than destined to admit the passage of food into them.

Fig. 103.



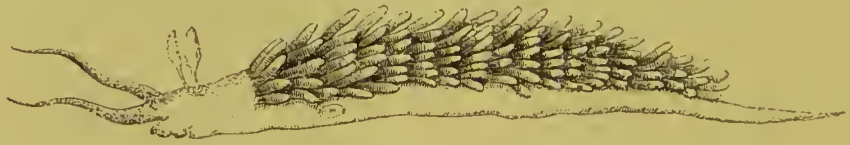
Digestive apparatus of *Annelida*:—A, *Aphrodite aculeata*; *a*, mouth; *b*, fleshy proboscis; *c*, central portion of digestive tube, representing the stomach; *d*, lateral appendages; *e*, anus.—B, *Hæmopis vorax*; *a*, mouth; *b*, lateral sacculi of the stomach; *c*, two large terminal cæca; *d*, intestine:—C, *Aulostoma nigrescens*; *a*, mouth; *b*, cæca; *c*, intestine.

156. From these forms we might gradually ascend towards the more complex digestive apparatus of Insects and Crustacea; but we shall first revert to that of the lowest Mollusca, as the simplest case in which the division of the canal into stomach and intestine is clearly marked out.

This is well seen in the *Bryozoa* (Fig. 49), in which, as in the Hydra, the whole process of digestion may be watched, owing to the transparency of the tissues of the animal. The digestive stomach (*c*) is here separated from the comparatively narrow intestinal tube, by a valvular orifice (*f*), or true 'pylorus;' and whilst the whole process of solution takes place in the former division of the canal, whose walls are beset with secreting follicles (*h*) that pour forth a bile-like fluid, the latter seems to have little to do, save to convey to the anal orifice (*l*) at the mouth of the polype-cell the excrementitious particles which are to be ejected from it. The same essential type is retained through the whole of the Molluscous series: the principal advance being shown (Fig. 50) in the higher development of the liver, by the withdrawal of its follicles from the parietes of the stomach, and by their aggregation into distinct glands which discharge their secretion into the upper part of the intestinal tube; in the development of a rudimentary pancreas (in the Cephalopoda); and in the increased length given to the intestinal portion of the tube, which usually makes several 'convolutions' before it finally terminates at the anus.—The same is the mode of advance which presents itself in the higher Articulata; among which the digestive apparatus of the Crustacea (Fig. 58, *c*, *d*, *e*) presents the greatest resemblance to that of Mollusca, whilst that of Insects (Fig. 57, *c*, *d*, *e*) is remarkable for the very low grade of development of the liver, which only makes its appearance in the form of a small number of cæcal tubuli (*f*, *f*) discharging their contents into the intestine. As yet no distinction between the 'small' and the 'large' intestine presents itself; this being only manifested fully in the higher Vertebrata.

157. It is interesting to observe that, among the higher tribes of both the Molluscous and the Articulated sub-kingdoms, we should find examples of reversion to that lower type of conformation of the digestive apparatus, which is manifested in its extension into cæcal prolongations that radiate into parts of the body remote from the proper digestive sac, and in the diffusion of the glandular apparatus over the whole or the greater part of their surface. This is the case with the *Nudibranchiate* Gasteropods (Fig. 104), in which the alimentary canal sends off as many cæca as that of the *Planariæ* (Fig. 101), each one of them, however, terminating in one of the dorsal papillæ, and being there surrounded by a group of hepatic cells, the liver being thus subdivided (so to speak) amongst them all. So among the Crustacea, we find the curious group of *Pycnogonidæ* especially characterized by the extension of the digestive cavity into the

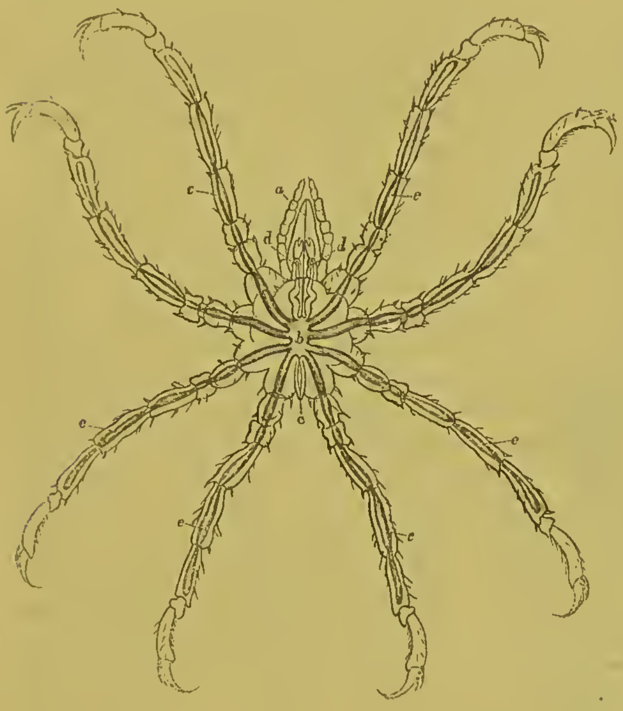
FIG. 104.



Eolis Inca, a Nudibranchiate Gasteropod.

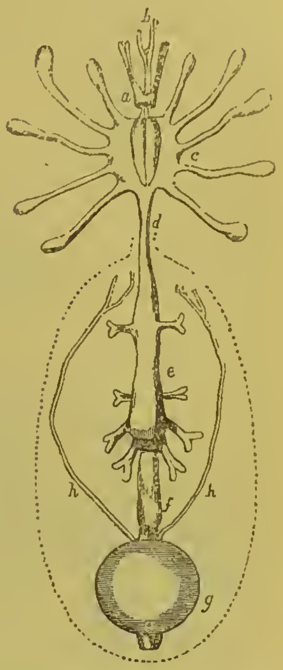
articulated members, almost to their extremities (Fig. 105), and by the spreading-out of the hepatic cells over the entire surface of these cæca;

FIG. 105.



Ammothea pycnogonoides;—*a*, narrow œsophagus; *b*, stomach: *c*, intestine; *d*, digestive cæca of the feet-jaws; *e e*, digestive cæca of the legs.

FIG. 106.



Digestive apparatus of *Mygale*:—*a*, cephalic ganglion; *b*, bifurcated origin of œsophagus; *c*, stomach with lateral cæca passing into the limbs and palpi; *d*, portion which traverses the abdominal peduncle; *e*, dilated intestine, receiving biliary vessels; *f*, small intestine; *g*, cæcal enlargement, receiving the urinary vessels *h*, *h*.

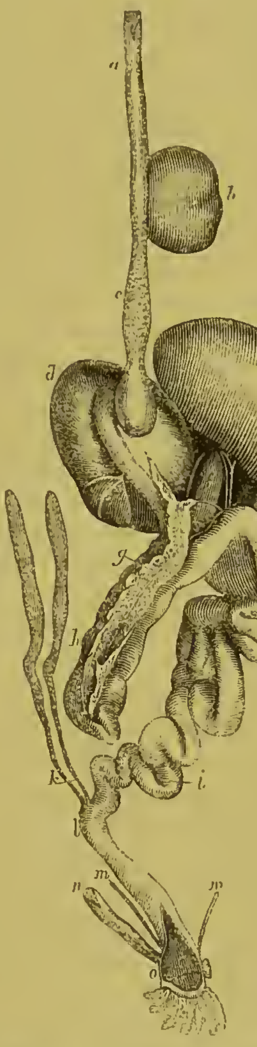
and it is peculiarly worthy of note, that whilst the alimentary matter passes into these extensions, and is conveyed by a continual flux and reflux through them (as microscopic observation shows) into the immediate neighbourhood of every portion of the body, the special circulating apparatus presents its very lowest grade of development (§ 231). An approximation to the same structure is seen in the cæcal prolongations of the digestive cavity, which pass into the thoracic members of the *Arachnida* (Fig. 106, *c*); these, however, would not seem to possess any special secreting function, a distinct biliary apparatus being found in the abdomen. But in certain *Acaridæ* we return to a condition even lower than that of the Pycnogonidæ; the parietes of the cæcal prolongations of the digestive cavity not being distinctly separable from the tissues around, and not even the rudiment of a proper circulating apparatus being distinguishable.

158. The digestive apparatus of Vertebrated animals may be considered as carrying onwards the general plan which has been seen to prevail in the Molluscous sub-kingdom. Thus in *Fishes*, there is usually a well-marked distinction between the stomach and the intestinal tube; the

liver attains a high development, and is completely withdrawn from the parietes of the alimentary canal; and the pancreas, also, begins to appear as a distinct gland, instead of being a mere collection of cæca clustering around the digestive cavity. In the *Amphioxus*, however, we see a reversion to a very inferior type; the digestive portion of the alimentary canal (Fig. 127, *i, i*) being a short tube of nearly uniform size throughout, which commences behind the pharyngeal respiratory apparatus, and runs backwards almost in a straight line to the anal orifice, receiving in its passage the fluid discharged by the simple large cæcum, which is the only rudiment of the liver. In the *Cyclostomi* the stomach is merely a dilated portion of the tube, which lies in a straight line between the œsophagus and the intestine; but in nearly all the higher Fishes, both Osseous and Cartilaginous, it forms a large cavity (Fig. 126, $_2$) which lies out of the course of the alimentary canal, and is adapted to retain the food while the process of solution is being carried on. It is usually separated from the intestine by a narrow 'pyloric' orifice; and it is also generally divided from the œsophagus by a 'cardiac' valve, the aperture of which, however, is very wide, so as to admit the food which is swallowed in an undivided state, and does not completely prevent its regurgitation. Indeed it seems common for Fishes to disgorge the shells and other indigestible parts of their food through their mouths, like Polypes; and there are some (especially of the *Carp* tribe) in which a sort of *rumination* takes place, the food being sent back to the pharynx to be masticated by the pharyngeal teeth, and then returning to the stomach to undergo its final digestion. The intestinal tube is usually short and almost destitute of convolutions, as well as of nearly uniform diameter throughout, so that the distinction between the small and the large intestine is only marked (and this not constantly) by the ileo-colic valve. The surface of the mucous membrane lining the canal is considerably extended, however, by being thrown into *rugæ* or wrinkled folds, more or less projecting; these in the Osseous Fishes have seldom any great regularity of arrangement; but by the great projection and spiral continuity of one of these folds, the real length of the intestinal tube is greatly increased in the higher Cartilaginous Fishes, just as a spiral staircase is much longer than the cylindrical cavity within which it winds.—In the omnivorous tadpoles of *Batrachian Reptiles*, the alimentary canal is of great length, and forms numerous convolutions in the abdominal cavity; but the stomach is narrow and elongated, the intestinal tube is of nearly equal size throughout, and the boundary between the small and the large intestine is not distinctly marked. This condition is retained in many of the *Perennibranchiata;* but in the adult condition of the Frog and its allies, a nearer approach is exhibited to the character presented by the alimentary canal in the higher *Reptiles,* most of which are carnivorous. In these we usually find the gastric dilatation larger, and more completely distinguished from the intestinal tube; although the intestine is relatively much shorter, yet the extent of its mucous surface is augmented by *rugæ* and *villi;* and the small intestine is now more constantly separated from the colon, by a valvular constriction. It is in the vegetable-feeding Turtles, that we find the intestinal tube possessing the greatest length, and presenting the greatest difference of diameter in its two divisions; and in most of these, as well as in some other Reptiles, the large intestine has a cæcal dilatation at its commencement.

159. In *Birds*, the length of the alimentary canal varies greatly in the different families, in accordance with their habitual diet, being greatest in the granivorous and frugivorous tribes, and least in the predaceous: there is, however, a certain general plan of conformation, to which the variations may be all referred. In nearly all the members of this class, the food is delayed in a receptacle formed by the dilatation of some part of the mouth, pharynx, or œsophagus, before it passes into the stomach; and in this receptacle it sometimes undergoes a sort of preliminary digestion. In the Pelican we find it in the form of a wide pouch suspended from the lower jaw, the two halves of which bone are not united at the symphysis, so that the pouch is enormously dilatable; in the Swift and other birds that catch insects on the wing, a similar distensibility exists in the membranous wall of the fauces; in the Cormorant and other fishing birds, it is the wide œsophagus which serves as the receptacle; but in the Granivorous birds, as well as in many others which take in a large quantity of food at once, we find a pouch termed the 'crop' (Fig. 107, *b*), developed from the side of the gullet, into which the food passes when it is first swallowed, and in which it lies for some time; during which it is moistened by a secretion copiously poured out from glandular follicles in its walls, and is thus prepared for the further stages of the digestive process. Below the crop, the œsophagus is usually again dilated, before its termination in the gizzard, into another cavity, known as the 'proventriculus' (*c*), from the walls of which the true gastric fluid is poured out upon the food that is delayed in it: this may be considered as the first or cardiac portion of the true gastric cavity; whilst the 'gizzard' (*d*) or muscular sac which succeeds it, corresponds with its second or pyloric portion. The gizzard is usually a somewhat lengthened sac, having its intestinal orifice, as well as that by which it communicates with the proventriculus, at its upper part. In

Fig. 107.



Digestive apparatus of *Common Fowl*:—*a*, œsophagus; *b*, ingluvies or crop; *c*, proventriculus; *d*, gizzard; *e*, liver; *f*, gall-bladder; *g*, pancreas; *h*, duodenum; *i*, small intestine; *k*, cæca; *l*, large intestine; *m*, *m*, ureters; *n*, oviduct; *o*, cloaca.

those whose food requires the aid of mechanical reduction for its solution, the walls of the gizzard are very thick and muscular, and its fibres radiate from two central tendons situated on opposite sides of the cavity, which is lined by a horny epithelium of remarkable toughness. The triturating power of the gizzard is frequently much increased by the presence of hard angular stones, which the bird occasionally swallows, and which are retained in its cavity. In Birds, however, whose food consists of flesh, fish, succulent fruits, or other substances easily reduced, the muscular structure is so little developed, that the original character of the 'gizzard' is entirely wanting. The intestinal tube varies considerably in length, and also in the degree of definiteness of the division between the small and the large intestines. At no great distance from the stomach, it receives the secretions of the liver (*e*) and of the pancreas (*g*); the former gland, which is of moderate size, possesses a gall-bladder (*f*), in which the bile can be stored up when not required for use, and yet has a second excretory duct, by which the bile can be poured direct into the intestinal tube; the latter, which is now much increased in size, and has attained a higher grade of glandular development, still pours forth its products, sometimes by two ducts, and in other cases by three. After a larger or smaller number of convolutions, the intestinal tube terminates in the cloaca (*o*); first, however, receiving the products secreted from one or two cæcal appendages (*k*) whose opening into the canal is considered to mark the boundary between the small and the large intestines (*i* and *l*).

160. The length and complexity of the alimentary canal in the *Mammalia*, as in Birds, vary in accordance with the diet on which the several tribes are adapted to exist; and no part exhibits a greater diversity of conformation than does the stomach,—even putting aside that peculiar apparatus which has been already described (§ 150) as concerned in the preparation of the aliment in the Ruminantia. Thus in the carnivorous and insectivorous Mammals, whose food is easy of solution, and consequently requires to be but little delayed for the digestive operation, the stomach is usually simple in its form, being a mere dilatation of the alimentary canal, and lying nearly in the direction of its course; but in proportion as the food departs more widely in its composition from the body itself, and is less capable of reduction by the gastric fluid, do we find (in most cases at least) the dimensions of the stomach increasing, and its form undergoing alteration; so that it more and more presents the character of a *diverticulum,* into which the aliment is turned aside, and in which it is retained during the time required for its subjection to the solvent power of the gastric juice (Fig. 62, *g*). The difference in form is principally given by the increased development of the large or left-hand extremity of the stomach, which thus becomes a sort of cæcal dilatation off the line that connects the cardiac and pyloric orifices; and not unfrequently this portion of the stomach is separated from the other by an incomplete partition. In addition to this, numerous smaller cæca are frequently developed in connection with the principal cavity; whilst in many *Cetacea* we find a succession of constrictions intervening between the principal gastric cæcum and the pyloric orifice, which partially divide the entire stomach into numerous cavities, all of them to be traversed by the food during its passage from the œsophagus to the intestine. The small intestine is chiefly remarkable for the great length to which it

extends in some of the herbivorous Mammalia, and for the increase of its mucous surface by 'valvulæ conniventes,' which are deep folds of membrane, succeeding one another at tolerably regular intervals, but not embracing above two-thirds of the circumference of the tube. In nearly all Mammals, save in the *Cetacea* (which exhibit a return to a fish-like inferiority in this respect), a well-marked distinction between the small and the large intestine is manifested, not only by the presence of the ileo-cæcal valve, but also by that difference of diameter from which these two divisions of the canal derive their names. The large intestine is here not only larger in proportion to the small, but is longer, than in the lower Vertebrata; and in many Mammals, as in Man, a sacculated character is given to the colon by the peculiar arrangement of its muscular bands, so that the extent of its lining membrane is greatly increased. The cæcal enlargement, in which the ileum terminates and the colon commences, is frequently of great size, especially in herbivorous animals; being sometimes larger than the stomach, as is the case in the Horse; or even many times larger, as may be seen in some of the *Rodentia*. The *villi* (Fig. 108), which in all the lower Vertebrata are dispersed over the surface of the large as well as of the small intestine, are now limited to the latter; whilst from the great number of glandulæ contained in the former, and from the change in the character of the contents of the alimentary canal which shows itself when they arrive there, it seems probable that whilst the small intestine is the part of the canal in which *Absorption* specially takes place, the large is particularly destined for *Excretion*.

161. Thus then, we see, that although the development of the Digestive apparatus is subjected, perhaps more than that of any other portion of the apparatus of Organic life, to variations which are immediately connected with the purposes to which it is to be subservient, a gradual *specialization* can be most distinctly traced, when we take a general survey of the succession of forms which it presents among the principal groups of animals. For, in its lowest condition, we have seen it to consist of a simple cavity excavated in the tissues for the reception of alimentary substances, which, when reduced to the state of solution (chyme), are taken up from every part of its walls, and find their way, without any special system of canals, into the parts of the body most remote from it: whilst the indigestible matters are ejected by the same orifice as that by which the food was taken-in. Next, we find the digestive sac furnished with parietes of its own, and suspended within a visceral cavity, with which it is at first in free communication; going a step further, we find this communication closed, but the digestive sac itself extended into remote portions of the organism; and, in still higher forms, the liquid (chyle) which transudes into the visceral cavity, instead of the immediate product (chyme) of digestion, is that which is applied to the purposes of nutrition. Next, we find the digestive sac with its single orifice changed into a canal, provided with a second orifice, through which the indigestible and fæcal matters are ejected. Next, we find the stomach more or less distinctly separated from the intestinal tube: and the former becomes possessed of special endowments which are not shared by the latter, the gastric fluid being secreted by its walls alone, and the secretion of the liver being either poured into it, or into the first portion

of the intestine. Next, we find the mucous surface of the intestinal canal considerably extended by folds and duplicatures; and these are thickly set with *villi*, each of which not merely contains a copious network of blood-vessels, but also includes the commencement of one of the special absorbents or 'lacteals' peculiar to Vertebrated animals. Next, we find the distinction between the small and the large intestine gradually becoming more clearly marked, and each part characterised by its own peculiarities; whilst at the same time, the concentration of structure is still further indicated by the greater extension of the mucous surface within the canal, by the augmented number of villi in the small intestine, and by the increase of the glandulæ and follicles in the large.

162. Now in its general outlines, the history of the Embryonic development of the Digestive apparatus in the higher animals closely corresponds with this; but the entirely different mode in which the alimentation of the embryo is to be accomplished, involves a considerable variation in the particular method adopted. The embryonic cell, when it is first distinguishable in the ovum, lies in the midst of a store of nutriment (the yolk) provided for it by the parent; and this it begins to draw-in, like the simple cells of the lowest Entozoa, which it resembles in grade of development and in its conditions of existence (§ 138), by imbibition through its cell-wall. The successive broods of cells produced by fissiparous multiplication, are at first nourished after the same fashion; but these soon tend to spread themselves in the form of a membranous expansion around the yolk, and thus to include it completely within the embryonic cavity. This cavity may be likened to the stomach of the Hydra, in every respect save that it has no orifice; but this is not needed, since it is already filled with the requisite supply of aliment. The further introduction of this into the embryonic tissues, is accomplished at first by the cellular layers of the germinal membrane; but blood-vessels are soon developed, which thenceforth are the special channels for its reception and conveyance. This cavity, however, serves but a temporary purpose,—in this respect corresponding with the cotyledons, by which nutriment is received into the embryo of the higher plants; and the permanent digestive apparatus commences in the more advanced embryo, as a small portion of the temporary vitelline sac, that is gradually detached from it, like the stomach of the budding *Hydra* from that of its parent. The form which this detached portion at first exhibits, is that of a simple tube, closed at both extremities, whilst its middle portion remains connected with the yolk-bag. An oral and an anal orifice are then formed; and the tube thus comes to present the characters of the alimentary canal of the lower Articulata. The next grade in development is the evolution of the stomach, which first shows itself as a projection of the tube towards the left side; and the accessory glands, the liver and pancreas, soon make their appearance, reminding us in their earliest condition of the grade of development which they permanently exhibit in the lower animals (CHAP. IX.) The short straight tube gradually increases in length, and is thrown into convolutions, that part being most increased in length which remains of the smallest diameter; and thus arises the difference between the small and the large intestine. The folds of the mucous membrane, the villi, and the glan-

dular apparatus, which are the parts most restricted to higher animals, are the last to appear in the course of their development.

163. We have now to consider the proper *Function of Digestion*, which may be said to commence with the introduction of the food into that part of the alimentary canal, in the walls of which is secreted the fluid destined for its solution. In the higher animals, this secretion is restricted to the gastric cavity or stomach; and hence it is named the 'gastric juice.' The only chemical change which the food appears to have undergone, before being submitted to this, is that which is effected by the admixture of Saliva in the mouth; a peculiar animal principle contained in this fluid having the power, like the *diastase* in Plants, of converting starch into sugar. The process thus commenced in the mouth, is retarded in the stomach, the acid character of the gastric fluid being unfavourable to it; it is recommenced, however, in the intestinal canal, after that acid has been neutralized by the alkali of the bile and pancreatic fluid. The great purpose of the *gastric* digestion appears to be, to dissolve the *albuminous* and *gelatinous* constituents of the food; and, by the withdrawal of these, the remainder are usually reduced to a state of fine division, in which they are afterwards more easily acted-upon. In regard to the constitution of the gastric juice, there is at present much diversity of opinion; and it does not seem improbable that it may vary in different animals. It appears essentially to consist, however, of a free acid (either the hydrochloric, acetic, or lactic, but generally the first) which is the real solvent; and of an animal principle in a state of change, which acts as a *ferment*, and disposes the organic compounds to solution. Water slightly acidulated with these acids, is capable of dissolving albuminous compounds with the aid of a high temperature; but if a solution of 'pepsin' (which is the animal matter obtained by macerating the stomach of a pig in cold water, after it has been repeatedly washed) be added, the acid solvent will then be able to act efficaciously at the ordinary temperature of the body. The solvent action of the gastric juice is aided by the movements of the walls of the stomach, which are produced by the successive contractions and relaxations of their muscular fibres. The purpose of this motion is obviously to keep the contents of the stomach in that state of constant agitation, which is most favourable to their chemical solution; and particularly to bring every portion of the alimentary matter into contact with the lining of the stomach, so as to subject it to the action of the solvent fluid which is poured forth from it. Thus, little by little, the reduction of the alimentary materials to the homogeneous pulpy mass termed *chyme* is accomplished; this escapes into the intestine, as fast as it is formed, through the pyloric orifice, which closes itself to solids, but allows liquids to pass; whilst the solid residue is continually subjected to the same action, until its solution has been effected. There is no doubt, however, that a portion of the nutritious matter dissolved by the gastric fluid is at once absorbed into the blood-vessels of the stomach, without passing either into the intestinal tube, or into the special lacteal system of vessels.—That the action of the gastric juice is in all respects one of a purely chemical nature, there can be no longer any question. When drawn direct from the stomach of Man or of the lower Mammalia, it is found to possess the power of dissolving various

kinds of alimentary substances, provided that these are submitted to its agency at a temperature equal to that of the body, and are frequently agitated. The solution appears to be in all respects as perfect as that which is naturally effected in the stomach; but a longer time is required to make it,—a difference which is easily accounted-for, when the impossibility of fulfilling *all* the conditions under which gastric digestion takes place, is borne in mind. The quantity of food which a given amount of gastric fluid can dissolve, is limited; precisely as in the case of the acidulous solution of 'pepsin,' or 'artificial gastric juice,' whose solvent power is chiefly regulated by the quantity of acid which it contains, the same quantity of pepsin being capable of 'disposing' the solution of many successive amounts of the substance to be acted-on, provided that acid be added as required.

164. The *Chyme* which passes into the intestinal tube, is commonly a greyish, semifluid, and homogeneous substance, possessing a slightly acid taste, but being otherwise insipid. When the food has been of a rich oily character, the chyme possesses a creamy aspect; but when it has contained a large proportion of farinaceous matter, the chyme has rather the appearance of gruel. The state in which the various alimentary principles exist in it, has not yet been accurately determined; the following, however, may be near the truth. The albuminous compounds, whether derived from the Animal or from the Vegetable kingdom, whether previously possessing the form of fibrin, of casein, of glutin, &c., are reduced by solution to the condition of Albumen; but a part of these compounds may still remain undissolved in the chyme of the intestine. Gelatine will be dissolved, or not, according to the previous condition of the substance containing it; for if this be a tissue which does not readily yield gelatine to hot water, the gastric fluid will have little influence upon it. The gummy matters of plants are dissolved, when they exist in a soluble form; but starch is not changed unless it has been previously acted-upon by the saliva, save in the case of the Granivorous Birds and Ruminant Mammals, in which the provision for the mechanical reduction of this element of the food is greater than in other tribes. Sugar, whether introduced as such, or formed by the transformation of starch, is undoubtedly reduced to a state of complete solution, and is probably taken-up by the blood-vessels as fast as it is dissolved. Oily matters, whether of animal or vegetable origin, are reduced to minute particles, and these are dispersed through the other constituents of the chyme. Most other substances,—as the woody fibres, all the firmer cell-walls, and the resinous matters, of Plants,—the horny matter, yellow fibrous tissue, epidermic and other thick-walled cells, of Animals,—pass unchanged from the stomach, undergo no subsequent alteration in the intestinal canal, and form part of the fæcal matter which is discharged from it.

165. On passing into the small intestines, the Chyme soon becomes mingled with the *Biliary* and *Pancreatic* secretions, and with the *Succus Entericus*, which appear to effect important changes in its character, though the nature of their respective agencies has not yet been clearly made out.* It may, however, be pretty certainly stated, that by the

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* The statements of M. Cl. Bernard respecting the special and exclusive emulsifying power of the Pancreatic fluid, have not been substantiated by the results obtained by other experimenters. See on this point the Author's "Principles of Human Physiology" §§ 452—455; and the "Brit. and For. Med.-Chir. Rev.," Jan. 1854, pp. 61—66.

excess of alkali which they contain, they neutralise the acid of the gastric juice, and that the conversion of the starch into sugar, which was interrupted in the stomach, now recommences, and is probably carried on while the food is passing through the small intestines; and further, that either by their separate or their combined actions, the fatty matter of the chyme is reduced to that state of fine division which is known as an 'emulsion,' and is thus rendered capable of being received into the absorbents; whilst the solution of the albuminous matters is completed. Thus, then, during the continued passage of the food along the upper part of the alimentary canal, the process of reduction and solution are still carried on; those operations being gradually performed in the intestine, which would have interfered with the digestion of albuminous matters if performed in the stomach; and the prolongation of this process being also the means of preventing the too rapid entrance of those saccharine and oily matters into the blood, which are only taken into it with a view to being speedily eliminated by the respiratory process, for the maintenance of the animal temperature. It is chiefly in warm-blooded animals, that we find the farinaceous or starchy substances, supplied by plants, entering largely into the composition of the food; and notwithstanding the evidence we possess that they are actually received into the vessels, yet there is a difficulty in detecting them under any form in the blood or chyle, in the healthy condition of the system. It is obvious, then, that their removal from the intestinal canal by the process of absorption must take place slowly; and thus we seem to have the explanation of the prolongation of the intestinal tube in herbivorous animals. It has been supposed that the contents of the intestinal canal are subjected to a sort of second digestion in the cæcum, for the purpose of dissolving any albuminous matters which have not been previously reduced, especially in those animals in which the cæcum is of large size in proportion to the stomach; and this idea seems to derive confirmation from the fact, that the secretion of the cæcum has been found to possess an acid reaction. It cannot, however, be at present regarded as more than a probable hypothesis.—The residuary undigested portions of the food, mingled with the excrementitious portion of the biliary and pancreatic secretions, together form the principal part of the fæcal matters which are discharged from the large intestine; but there is strong reason to believe that the putrescent matter, which, in the Mammalia especially, gives the peculiar odour and appearance to the excrement, is not derived from either of these sources, but is a real excretion, separated from the blood by the glandular follicles that are so thickly set in the intestinal walls, and especially at the upper part of the large intestine.

CHAPTER IV.

OF ABSORPTION AND IMBIBITION.

1. *General Considerations.*

166. THE process by which the alimentary materials, whether in their original fluid form (as in the case of Plants), or after they have been reduced to that form by the digestive process (as in Animals), are introduced into the living body, is termed *Absorption.* Before considering the particular conditions under which this operation is performed in the different classes of Organised beings, it will be right to consider what is its essential character, and how far Physical principles can be applied to its elucidation.—It was formerly the general opinion that Absorption is always effected by vessels, the open mouths of which, being in contact with the fluid, might imbibe it by capillary attraction, suction, or other like agencies; and hypothetical 'absorbent vessels' were inferred to exist in all beings, even in the simplest Cellular Plants, as the channels whereby fluids are received at the surface and conveyed into the interior. But it has been shown by minute Anatomical inquiry, that in no one instance are absorbent vessels thus brought into immediate relation with the fluid to be received by them, but that the transmission always takes place in the first instance through some tissue of a membranous character; and further, that in a great number of cases, vessels are not concerned in the process at all, the fluid being at once received into the tissues which it is destined to nourish. Thus, we shall find that neither in the roots of Plants, nor in the walls of the alimentary canal of Animals, do the absorbent vessels commence in open mouths; but that all the fluid which enters them, must first traverse the membrane which covers their extremities; whilst in the lowest members of both kingdoms, and in the early embryonic condition of the higher, the external investment, or that reflexion of it which lines the digestive cavity (§ 122), has an equal power of imbibition throughout its entire surface, and communicates a portion of that which it has taken-up to the tissues in contact with it, whence it is progressively transmitted to the more remote parts,—and this without the aid of any system of vessels, either for the Absorption or for the Circulation of nutritive fluid. And even in the most elaborately-constructed organisms, we find that a considerable portion of the tissues is nourished by the same kind of imbibition,—not, however, from the external surface, or from the walls of the digestive cavity, but from nearer sources of supply. Thus the substance of proper cellular *Cartilage* is entirely nourished by imbibition from the blood-vessels which bring the nutriment to its surface and edges; the dense tissue of *Bones* and *Teeth* is in like manner traversed by nutritious fluid, which is drawn from the vessels of the nearest vascular canal or cavity; and the *Epidermic* and *Epithelial* tissues, which cover the surfaces and line the cavities of the body, must derive their nourishment from vessels ramifying on the

opposite side of the basement-membrane whereon they rest.—Thus it appears that the first introduction of fluid into the organism by *Absorption*, is but a particular case of that *Imbibition*, which takes a most important part in its subsequent diffusion through the system, even when the most complete vascular apparatus exists; and it will be right, therefore, to consider in the first instance what are the physical conditions of Imbibition.

167. When any porous substance (not already saturated) is brought in contact with a liquid which has such a molecular attraction for its particles as to be capable of 'wetting' it, the liquid is imbibed by it, and, if the force of imbibition be strong enough, is speedily diffused through the whole mass. This force depends in part upon *the degree of attraction subsisting between the particles of the solid and those of the fluid;* and in part upon the size of the capillary pores or canals. Thus it was found by Professor Matteucci,* that when glass tubes of about three-fourths of an inch in diameter were filled with fine sand, previously dried, and introduced without pressure, and were immersed at their lower ends into the following liquids, the action of imbibition (which took place at first rapidly, then more slowly, and then ceased after about ten hours) raised the liquids in the tubes to the following heights respectively:—

Solution of carbonate of potash, ...	85	millimètres.
Solution of sulphate of copper, ...	75	,,
Serum of blood, ...	70	,,
Solution of carbonate of ammonia, ...	62	,,
Distilled water, ...	60	,,
Solution of common salt, ...	58	,,
Milk, ...	55	,,
White of egg diluted with its own volume of water, .	35	,,

When thick solutions of gum or starch, or fixed oils, were employed, scarcely any imbibition took place; and it was but little more, when strong saline solutions were used.—The degree in which imbibition is affected by the peculiar attractions subsisting between the solids and the liquids employed, is further illustrated by the following experiment. Three tubes, respectively filled with sand, pounded glass, and saw-dust, were immersed at their lower extremities in water, and three similar tubes in alcohol; the following were the comparative results:—

	Sand.	Pounded Glass.	Sawdust.
Alcohol	85 millim.	175 millim.	125 millim.
Water	175 ,,	182 ,,	60 ,,

Thus we see that, whilst the imbibition of the two liquids took place into the pounded glass in nearly an equal degree, the quantity of water drawn up by the sand was more than double that of the alcohol, whilst precisely the reverse effect obtained in the case of the sawdust, the quantity of alcohol imbibed being more than double that of the water.—That the force of imbibition is dependent in part upon *the size of the capillary channels*, was proved by the fact, that when the experiment was tried with two tubes, both holding pounded glass, but one of them containing twice as much as the other (the powder being finer, and the capillary channels being consequently more minute), water was found to rise in the fullest tube to 170 millim., in the same time which it occupied to rise to 107 millim. in the other.—*Temperature,* also, was found to have a remarkable influence upon the result; for two tubes, similarly prepared with sand, having had their extremities immersed in water, and having been kept, the one at 131° Fahr., and the other at 59° Fahr., the water rose in eleven minutes to 175 millim. in the former, whilst in the same period it only rose to 12 millim. in the latter. Hence we see that an elevation of temperature has not only a direct influence in augmenting vital activity, but that it assists in supplying an essential condition of that activity, by promoting the transmission of nutritive fluid through the textures.

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* "Lectures on the Physical Phenomena of Living Beings," translated by Dr. Pereira, pp. 21, et seq.

168. But further, when two liquids capable of mixing together freely, without chemical decomposition, are allowed to do so, there is a tendency in each to a uniform diffusion through this other. The laws of this 'Diffusion of Liquids' have been recently investigated by Prof. Graham (the discoverer of the law of the 'diffusion of gases'); and the following are some of the results obtained by him, which bear most directly upon the present subject.*—The phenomenon was studied by means of a simple apparatus, consisting of an open phial to contain the liquid to be diffused, which was immersed in a large jar of pure water. The diffusion was stopped, generally after seven or eight days, by closing the mouth of the phial with a plate of glass, and then raising it out of the water-jar; and the quantity of the liquid which had found its way into the water-jar (or the 'diffusion product,') was then determined by evaporating it to dryness. The characters of 'liquid diffusion' were first examined in detail in reference to common salt; and it was found that when the amount of diffusion from solutions containing 1, 2, 3, and 4 per cent., was compared, it varied nearly in the same proportions, being in each case about one-eighth of the whole amount, after a period of eight days. But here, too, temperature has a remarkable influence: for an elevation of 80° Fahr. was found to double the quantity of salt diffused in a given time.—Different substances possess this property of diffusibility in very varying degrees; thus when solutions of the following substances were employed, of the strength of 20 parts to 100 of water, the relative quantities diffused in a given time were as follows:—

Chloride of sodium, .	58·68	Crystallized cane-sugar,	26·74
Sulphate of magnesia,	27·42	Starch-sugar (glucose),	26·94
Nitrate of soda, . .	51·56	Gum-arabic, . . .	13·24
Sulphate of water, . .	69·32	Albumen, ...	3·08

The low diffusibility of albumen is very remarkable; and it is further to be noticed that if common salt, sugar, or urea (which is as highly diffusible as chloride of sodium) be added to the albumen under diffusion, they diffuse away from this as readily as from their aqueous solutions, leaving the albumen behind in the phial. So, when solutions of two salts are mixed in the phial, they diffuse out into the water-atmosphere separately and independently of each other, according to their respective individual diffusibilities. In comparing the diffusibility of different salts, it was found that equal weights of 'isomorphous' compounds, dissolved in ten times their weight of water, diffused themselves to the same amount. And further, one salt, such as nitrate of potash, will diffuse into a solution of another salt, such as nitrate of ammonia, as rapidly as into pure water; the solutions appearing to have that mutual diffusibility, which gases are known to possess (§ 266).—The properties of different substances in regard to their relative diffusibility, cannot but have an important influence on the course of the vital operations. Thus the low diffusibility of albumen obviously tends to the retention of the serous fluids within the tissues; whilst the high diffusibility of urea will favour its escape from them.

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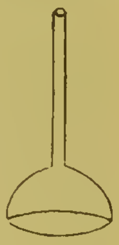
* "Philosophical Transactions," 1850, p. 1, et seq.

169. Both of these agencies,—the imbibition of fluids by porous solids, and the mutual diffusion of miscible liquids,—seem to be concerned in the production of that curious phenomenon, to which the term *Endosmose* was given by its discoverer, Dutrochet; and this process bears so close a resemblance to a vast number of the operations continually taking place in the living body, that it is scarcely possible to doubt that the same causes are in action in both cases. The following is a general account of the process in question.—If into a tube, closed at one end with a piece of bladder or other membrane, be put a solution of gum or sugar, and the closed end be immersed in water, a passage of fluid will take place from the exterior to the interior of the tube, through the membranous septum; so that the quantity of the contained solution will be greatly increased, its strength being proportionably diminished. At the same time, there will be a counter-current in the opposite direction; a portion of the gummy or saccharine solution passing through the membrane to mingle with the exterior fluid, but in much less quantity. The first current is termed *Endosmose*, and the counter-current *Exosmose*. The increase on either side will of course be due to the relative velocity of the currents; and the changes will continue until the densities of the two fluids are so nearly alike, as to be incapable of maintaining it. The greater the original difference (provided that the denser fluid be not actually viscid, but be capable of mixing with the other), the more rapidly and powerfully will the process be performed. The best means of experimenting upon these phenomena is afforded by a tube narrow above, but widely dilated below, so as to afford to the membrane a large surface compared with that of the superincumbent column, which will then increase in height with great rapidity. By bending this tube into the form of a syphon, and introducing into its curve a quantity of mercury, the force as well as the rapidity of the endosmose between different fluids may be estimated with precision. In this way it was ascertained by Dutrochet, in some of his experiments, that fluid might be raised against a pressure of no less than 4½ atmospheres, or nearly 70 pounds to the square inch.*—Although it is not universally true that the activity of the process is proportional to the difference in density of the two fluids (for in one or two cases the stronger current passes from the denser to the lighter), it seems to be so with regard to solutions of the



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* For further information on this curious subject, see the Art. 'Endosmosis' in the "Cyclopædia of Anatomy and Physiology," Dutrochet's "Mémoires Anatomiques et Physiologiques," tom. i., and Matteucci's "Lectures on the Physical Phenomena of Living Beings."

same substances (as gum or sugar) of different strengths. No endosmose takes place between fluids which will not mingle, such as oil and water; and very little between such as act chemically on each other. Although an organic membrane forms the best septum, yet it has been found that thin laminæ of baked pipe-clay will suffice for the evident production of the phenomenon; and that porous limestones possess the same property in an inferior degree.

170. Although it may not as yet be possible to explain all the phenomena of Endosmose upon physical principles, yet these will go so far towards it, that the general conditions of the process may be considered as well understood. Supposing that two mutually-diffusible liquids are on the opposite sides of a porous septum, which is not equally penetrable by them, then the one which is most readily imbibed will tend to occupy the capillary passages of the septum, and will thus be brought into contact with the liquid on the opposite side. This contact will permit the diffusion of that which has passed through the pores of the septum; and as fast as that which occupies these pores is removed by diffusion, so fast will it be renewed from the other side,—just as oil continues to ascend through the capillary channels in the wick of a lamp, so long as it is being dissipated by the combustive process at its summit. In this way, then, an Endosmotic current is produced, the force of which will depend upon the diffusion-powers of the two liquids, and upon the difference of the attractive powers which the capillary tubes of the septum have for each respectively. Thus, when a solution of sugar or gum is on one side of the septum, and water on the other, the water is the most readily imbibed: and consequently the chief mixture and diffusion of the liquids, the one through the other, take place at the surface of the septum in contact with the more viscid liquid. But at the same time, this liquid is tending to diffuse itself through the water which occupies the capillary channels of the septum; and, as it is not repelled by the septum, but is only attracted by it in a less degree than the water, a portion of it finds its way in a direction opposed to the principal current, and diffuses itself through the water on the other side, thus constituting Exosmose.—Thus it happens that the *direction* of the principal current, or Endosmose, will be determined by the attractive power of the septum for one or other of the liquids; though the diffusion-power of the liquids through each other will help to determine its *force*. When alcohol and water, for example, are separated by a septum composed of animal membrane, the endosmotic current will be from the water towards the alcohol, because the former liquid most readily 'wets' the membrane, and consequently tends most strongly to occupy its capillary passages: but on the other hand, when the separation is made by a thin lamina of caoutchouc, the endosmotic current is from the alcohol towards the water, because the former is most readily imbibed by the septum.

171. It has further been ascertained by the experiments of Matteucci, that when an organic membrane is employed as a septum, the rapidity of transmission is considerably affected by the direction in which the endosmotic current traverses the membrane. Thus when the skin of the Torpedo was employed, with a solution of sugar on one side of it, and water on the other, although there was always an endosmotic current from the water to the sugar, yet this current was strong enough to raise the in-

terior liquid to 80 degrees, when the water was in contact with the *internal* surface of the membrane, in the same time that was occupied by its rise to 20 degrees, when the *external* surface of the membrane was turned towards the water. Again, when the mucous membrane of the stomach of a dog was used as the septum, and its *external* (or muscular) surface was placed in contact with alcohol, the passage of water from the other side took place with such rapidity, as to raise the liquid in the tube to 130 degrees; whilst if the *internal* (or mucous) surface of the membrane was placed in contact with the alcohol, and the muscular surface with water, the current was only sufficient to raise the liquid 6 degrees in the same time: so that it is evident that the transudation of water takes place much more readily from the mucous lining of the stomach towards the outer side of the viscus, than in an opposite direction, in virtue simply of the physical properties of the membrane. In fact, according to Prof. Matteucci, the cases are very rare in which, with fresh membranes, endosmose takes place with equal readiness, whichever of their two sides is exposed to the water. The direction which is most favourable to endosmose through skins, is usually from the internal to the external surface, with the exception of the skin of the frog, in which the endosmotic current, in the single case of water and alcohol, takes place most readily from the external to the internal surface. But when stomachs and urinary bladders are employed, the direction varies much more in accordance with the nature of the liquids employed. This variation appears to have some relation to the physiological conditions in which these membranes are placed in the living animal; thus the direction most favourable to endosmose between water and a saccharine solution, is not the same for the stomach of a Ruminant as for that of a Carnivorous animal: as yet, however, no general statement can be made on this subject. When membranes are employed, that have been dried or altered by putrefaction, we either do not observe the usual difference arising from the position of the surfaces, or endosmose no longer takes place; thus affording another indication that it is to the physical condition of the perfectly-organised membrane, that we are to look for many of the peculiarities which are noticeable in the transudation of fluids through them.—The Exosmotic current does not bear any constant relation to the endosmotic, as may be easily comprehended from the preceding explanation; for if the liquids have a strong tendency to mutual diffusion, and the difference in the attractive power which the septum has for them respectively is not great, each may find its way towards the other, and a considerable exosmose may ensue, with very little change of level. The amount of the *ex*osmotic as of the *endo*smotic current, varies with the direction in which it traverses the membrane; thus when sugar, albumen, or gum was employed in solution, its transudation towards water took place most readily from the *internal* towards the *external* surface of all the skins examined by Matteucci;—a fact which is not without its significance, when it is remembered that it is in this direction that the secretion of mucus takes place on the skins of fishes, frogs, &c.

172. Applying these considerations to the phenomena of Imbibition of liquids into the tissues and canals of the living body, we shall have to enquire how far they are capable of being explained on the physical principles which have been now brought forwards.—It has been main-

tained by some that Absorption is a purely *vital* operation, because it does not occur save during the continuance of life. But this is not true; since imbibition will take place into dead tissues, though more slowly than into the same parts when living; and the difference of rate seems to be fully accounted-for, by the difference of the condition between a mass of tissue all whose fluids are stagnant, and another in which an active circulation is taking place. Thus it is stated by Matteucci, that if the hind-legs of a frog recently killed be immersed for some hours in a solution of ferrocyanide of potassium, every part of the viscera will be found to be so penetrated with the salt, that by touching it with a glass rod moistened with a solution of the chloride of iron, a more or less deep blue stain is the result. Now the same effect is produced much more speedily in a living frog; and it is easily proved that the imbibition takes place, in the latter case, into the blood-vessels, and that the salt is conveyed to the remoter parts of the body by the circulation, instead of having slowly to make its way by transudation through the tissues, as in the dead animal.—But further, not only does the movement of blood in the vessels promote the diffusion of liquid which has been already absorbed; it also increases the rapidity of the absorption itself in a very extraordinary degree. Thus, if a membranous tube, such as a piece of the small intestine or of a large vein of an animal, be fixed by one extremity to an opening at the bottom of a vessel filled with water, and have a stopcock attached at the other extremity, and be then immersed in water acidulated with sulphuric or hydrochloric acid, it will be some time before the acid will penetrate to the interior of the tube, which is distended with water; but if the stopcock be opened, and the water be allowed to discharge itself, the presence of the acid will be immediately discovered (by tincture of litmus) in the liquid which flows out, showing that the acid has been assisted in its penetration of the walls of the tube, by the passage of a current through its interior. Thus the continuance of the Circulation is obviously one of the most potent of all the conditions of Absorption; and the difference in the rate of the process in dead and living organisms placed under the same circumstances, may be accounted-for in great part, if not entirely, by the stoppage of the circulation in the former. All the circumstances which are laid down by Physiologists as favouring Absorption, are in strict accordance with the Physical principles which have been now explained. These circumstances are:—1. The ready miscibility of the liquids to be absorbed with the juices of the body. 2. The penetrability of the tissue through which the absorption takes place. 3. The absence of previous distension in the tissues or canals towards which the flow takes place. 4. The elevation of the temperature, within certain limits. 5. The vascularity of the tissue, and the rate of movement of the blood through the vessels.—And the results of experiments upon recently-dead membranes, which retain almost exactly the same physical conditions as those which they possessed during life, but have entirely lost their vital properties, seem most decidedly to indicate, that the relative facility with which different substances are absorbed, and the direction most favourable to their passage through the tissues, are determined in great part by the physical relations which those tissues (and the vessels that traverse them) bear to the liquid which is seeking to enter them. In this way, then, many of the phenomena of *selective* absorption are probably to be explained, especially in Plants and the lower Animals: and others will be shown to be due to the endowments of the cells which are in relation with the Absorbent vessels at their origin.

2. *Absorption in Vegetables.*

173. In the lowest orders of Plants, we find this function performed under its most simple conditions. Their substance is composed of vesicles more or less firmly united to each other, and but slightly altered from their original spheroidal form; and the envelope which surrounds them can seldom be regarded as a distinct structure, generally differing but little from the remainder of the cellular tissue. In all the *Algæ* (§ 24), the whole surface appears to be endowed with the power of absorption to nearly an equal degree; and although the semblance of a stem and roots presents itself in the higher orders, yet these seem to have no other function than to give the means of attachment to the frondose expansion. The preference of particular species of Algæ for particular rocks, cannot be fairly considered to indicate that any special absorption of the mineral particles takes place through their roots; it is much more probably due to the fact, that the materials of these rocks are in some degree diffused by solution through the neighbouring water: and something may be also attributable to the mechanical qualities of the rocks, as affording advantageous surfaces for attachment.—The difference in the situation inhabited by the *Lichens* (§ 25) appears to involve a separate appropriation of portions of their surface to the nutritive and reproductive functions, and a certain specialization of the absorbing organs. The upper surface of these plants, being exposed to the sun and air, becomes hard and dry, a condition which seems to favour the evolution of the fruit; whilst it is mostly by the lower surface, which is usually soft and pale, that the nutriment is introduced into the system. The latter is not unfrequently furnished with hair-like prolongations, which not only serve to fix the plant, but appear to be much concerned in the absorption of its aliment; being so much developed in some Lichens, which are located upon the ground, as almost to resemble roots.—In the *Fungi* we find the same evolution of the more special organ from the more general type. The lower forms of this group (§ 26) seem to imbibe their aliment by their whole surface; but in the more complex structures, in which the reproductive system is separated from the nutritive by the intervention of a stalk (as in the Mushroom), the *mycelium* at its base is prolonged into filaments, whereby the decaying matter, that constitutes the food of this remarkable group of plants, is introduced into the system. In some species, too, the whole surface is covered with hair, which may assist their very rapid development by absorption of fluid from the atmosphere. —In the *Mosses* and their allies (§ 27), we find a somewhat higher form of the same structure. From the base of the stem there usually proceed slender radical filaments, which sometimes ramify through the soil to a considerable extent; and other similar filaments are frequently developed from the sides of the stalk, and from the lower surfaces of the leaves. In Mosses that exist on rocks, however, these filaments are but little developed, and appear to serve rather for mechanical support, than for absorption of nourishment, which must in such circumstances be derived from the atmosphere through the leaves. These, as is well known, are

very permeable to fluid, so that the application of moisture will cause Mosses to recover the appearance of life after being long dried; and the same property enables these beautiful little plants to vegetate rapidly during a moist season, whilst their tenacity of life enables them to withstand a subsequent drought.—In ascending through these tribes of Cryptogamia, then, we may trace a gradual development of separate absorbent organs, and may observe the *specialization* of the function, by its restriction to one particular part of the surface, instead of being diffused over the whole. The absorbent filaments, however, are very inferior in their structure to true 'roots,' being little else than elongated cells, resembling the hairs with which other parts of the surface are covered; and they seem to absorb fluids equally throughout their entire length. Further, we find that, when these special organs are not developed, or are insufficiently supplied with nutriment, the general surface can take-on its original function, and thus supply the deficiency.

174. It is in the *Ferns* (§ 28) that we first meet with a regular 'descending axis' of growth, from which the absorbent fibres are given off; and this is evolved in its completest form in the *Phanerogamia* (§ 29). In these Vascular plants, moreover, it seems to be through the newly-formed succulent extremities alone, that fluid is admitted; and the function is, of course, more actively performed by them, in proportion to the diminution in the amount of surface they expose. The *root* presents a great variety of forms in different plants; there are, however, some parts which are essential, and others that are merely accessory. The simplest form, as well as the most essential part, consists of single fibres; these occasionally exist alone (as at the base of 'bulbs'), but more often proceed from ramifying branches of woody texture (as in most trees and shrubs), or from 'tubers' (as that of the turnip). Each radical fibre is of a structure far more complex than the absorbent filaments just mentioned as existing in Cellular plants; for it is a cylinder, in whose axis lies a bundle of fibro-vascular tissue, whilst its exterior is composed of firm cellular parenchyma; at its free termination, however, the extremities of the vessels are covered with loosely-formed cellular tissue, through which the fluid passes into them. The *spongiole*, as this point has been termed, is sometimes spoken-of as a distinct organ; but it is nothing more than the growing point of the root, which, with a few exceptions, lengthens only by additions to its extremity. The soft lax texture of the newly-formed part causes it to possess, in an eminent degree, the power of absorption; but as the fibre continues to grow, and additional tissue is formed at its extremity, that which was formerly the spongiole becomes consolidated into the general structure of the root, and loses almost entirely its peculiar properties. That it is to the spongioles that the principal absorbing power of the root is due, was fully proved by the experiment of Senebier. Having fixed two roots in such a manner, that the extremity of one was in contact with water, whilst of the other every part was immersed except the extremity, he found that the first root absorbed nearly as much as usual, whilst the second scarcely took up a sensible quantity. It is not improbable that the relative absorbent power of the spongioles and of the general surface of the root, may vary in different plants, according to the character of the texture of each, and the situation in which it grows; but it appears to be a general fact, that, in Vascular plants, the spongioles

are the organs *specially* destined for introducing the fluid nutriment into the system.

175. There are evident limits to the supply of alimentary materials to the roots of Plants, so long as they remain in the same spot; and some change must take place to ensure its continuance. As the Plant cannot remove itself to a new situation, its wants are provided-for by the simple elongation of its radical fibres; and their extension takes place, not by increase throughout their whole length, but by addition of fresh tissue to their points. This addition, being made in the direction of least resistance, enables the fibrils to insinuate themselves into the firmest soil, and even to overcome the obstacle presented by solid masonry; for however narrow the crevice may be into which the filament enters, the subsequent expansion of the tissue by the infiltration of fluid is so great, as to enlarge the opening considerably, and even to rupture masses of stone. This tendency to increase in the direction of least resistance, will also evidently cause the root to grow towards a moist situation; and by keeping this in view, many of the facts regarding the so-called *instinct* of plants, which at first sight appear so remarkable, may be satisfactorily explained. Thus, it was noticed, when the water of the New River was conveyed through wooden pipes, that if these pipes were carried within thirty yards of trees, they were very likely to be in time obstructed by their roots; which 'found' the joints, and then spread out in 'foxtails' of fibres, two or three feet long. It is well known to the agriculturist, that the course of large drains, even at a considerable depth in the ground, is liable to be interrupted by the extension of roots, not only from trees, but also from apparently insignificant plants. Thus at Saucethorpe, in Lincolnshire, a drain nine feet deep was filled-up by the roots of an elm-tree, which was growing at upwards of fifty yards from the drain: a deep drain outside the garden-wall at Welbeck was entirely stopped by the roots of some horse-radish plants, which grew seven feet into the ground: and at Thoresby Park, a drain fourteen feet deep was entirely stopped by the roots of gorse growing at a distance of six feet from it.*—In other cases, we must attribute the result to the dispersion of vapour through the atmosphere in a particular direction. Thus, in a case which fell under the Author's cognizance, a lime-tree, which grew at the distance of about fifteen feet from the shaft of a well, sent a single long root through the soil, in a direct line towards a point of the shaft at which there was a small aperture left by the deficiency of a brick : this aperture was at a height of eleven feet above the usual level of the water in the well; and the root, having passed through it, divided into a brush-like mass of fibres, which descended into the water, and formed a large mass in the lower part of the well. Again, in a peculiar case known to the Author, in which one tree grew upon the trunk of another, having originated from a seed deposited at about twelve feet above the ground, one of the large roots which it sent down, subdivided about two feet above the surface of the ground, instead of proceeding directly down to it, as did all the rest. Now this subdivision took place above a large stone, on the centre of which the root would have impinged, if it had continued to grow directly downwards; and it would appear as if its division, half proceeding to one

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* "Journal of the Royal Agricultural Society," Vol. I. p. 364.

side, and half to the other, was due to the direction given to its growth by the ascent of vapour from the soil beneath. On the same principle we are probably to explain the following case. "Near the waterfall at the head of the river Leven, in the Western Highlands, is the trunk of a decayed oak, rotten within, but alive on some parts of the outside. From one of these, a shoot grows out, about fifteen feet from the ground; and this shoot has protruded from its lower part a root, which, after having reached the ground (a bare rock), runs along the rock in a horizontal position, about thirty feet further, till it reaches a bank of earth in which it has embedded itself."*

176. The absorbent power of the Spongioles appears limited by the size of their pores; for if the roots be immersed in coloured solutions, they take up the most finely divided particles, leaving behind the larger molecules, which are only absorbed when the spongioles have been damaged. The pores are liable to be blocked-up by fluids which are of too viscid or glutinous a consistence to pass readily through them; and if the roots be immersed in a thin solution of gum or sugar or neutral salts, the watery particles are absorbed in the greatest degree, so that the portion which is left contains a larger proportion of the ingredient in solution. The power of *selection*, however, would seem to extend beyond this: since of two substances equally dissolved, some plants will take one, and some the other; whilst some neutral salts are rejected altogether. It does not appear that the selecting power is employed to prevent matter, which is capable of exerting a deleterious influence upon the plant, from being introduced into its tissue; for many substances are taken-up by the roots, which speedily put a stop to vital action, if opportunity be not afforded for their excretion. From the little that is at present known on the subject, it seems a reasonable inference, that the rejection of any particular ingredient of the fluid in contact with the roots, results either from an organic change effected by it on their delicate tissue (such as is proved by the experiments of M. Payen† to occur when tannin enters into the solution, even in very minute proportion), or from the want of molecular attraction between its particles and the substance of the spongioles. That some kind of relation between the living tissue and the crystalline character of the salt, is concerned in the selection, appears from the interesting results of the experiments of Dr. Daubeny on the absorption of mineral substances by Plants. He has found that, if a Plant naturally absorbs the compounds of any particular base, it may also take-up those of another base which are *isomorphous* with them (most vegetables, for example, absorbing the salts of Lime and Magnesia with equal readiness); whilst salts, however soluble, which have a crystalline arrangement different from theirs (such as those of Strontia), are not absorbed.‡—The *quantity* of fluid absorbed, and the *force* with which it is propelled upwards in the stem, vary not only in different species and individuals, but

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* "Gardeners' Magazine," Oct. 1, 1837.

† "Annales des Sciences Naturelles," Deuxième Série, Botan., Tom. III. p. 5, &c.

‡ "Linnæan Transactions," 1833.—Some recent experiments, however, by the same distinguished Chemist, indicate that potash and soda cannot be substituted, one for the other, in the vegetable organism, to any great extent; for the proportions of these two bases in the alkaline ash of barley are nearly the same, whether the soil in which the barley is grown be manured with potash or with soda, or be left without artificial addition. (See "Journal of the Chemical Society," Vol. V. p. 9.)

in the same plant at different periods of the year, and even of the day. The former seems intimately connected with the activity with which the other processes of vegetation are being carried on, and especially to depend upon the quantity of vapour transpired from the leaves (CHAP. VII.); all the causes which increase exhalation, may therefore be considered as stimulants to absorption also. The *vis à tergo* possessed by the ascending sap, is sufficiently proved by the celebrated experiments of Hales on the vine. By gages affixed to the stem during the 'bleeding-season,' when the sap rises rapidly, he found that a column of mercury 26 inches high, equal to a column of water of nearly 31 feet, might be supported by the propellent force of the absorbent organs; but if the upper part of the plant was cut off, this power soon diminished, and after a time ceased altogether.

177. There would seem much reason to believe, that the mere act of Absorption in this and other cases, is due to the physical property already referred-to, as possessed by many organised tissues,—viz. the capability of producing Endosmose (§ 169). The succulent extremities of the spongioles serve as the medium required for this process; but it may be reasonably enquired whence the other condition is furnished, namely, that difference in density of the fluids on the opposite sides of the septum, which is necessary for the commencement and continuance of the action. This is supplied, in the first instance, by the store of nutritious matter obtained by the embryo from its parent, and contained within its tissues; and, possibly, at a later period, when the plant is supporting an independent existence, by the admixture of a portion of the dense elaborated sap, with the crude and watery ascending fluid. If this be the true explanation of the phenomenon, a counter-current ought to exist, and an *exosmose* of the fluids within the system should take place into the surrounding medium. That this is actually the case, would appear from the fact, that an excretion of the peculiar products of the species may be often detected around the roots of the plant. The cessation of this action of admixture (a change evidently depending upon other vital actions) at the death of a plant, fully accounts for the non-continuance of endosmose; which is also checked if the superincumbent column of fluid be not drawn off by the leaves. It has been very justly remarked by Professor Henslow, that, "if we suppose the plant capable of removing the imbibed fluid as fast as it is absorbed by the spongioles, then we may imagine the possibility of a supply being kept up by the mere hygroscopic property of the tissue; much in the same way as the capillary action of the wick in a candle maintains a constant supply of wax to the flame by which it is consumed."* And this is probably the explanation of the fact, that absorption of fluid continues to take place into the open mouths of the vessels, when the upper part of a plant is cut off, and the divided extremity is immersed in water; for, so long as exhalation takes place from the leaves, so long will a demand for fluid be created in the vessels from which they draw their supply.

178. It is an axiom in Vegetable Physiology, which has been laid down by De Candolle, "that when a particular function cannot, according to a given system of structure, be sufficiently carried into effect by

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* Treatise on 'Botany' in the "Cabinet Cyclopædia," p. 177.

the organ which is ordinarily appropriated to it, it is performed wholly or in part by another." This is a single case of the general principle which has been already laid down (§ 110); and the reason that it is more evident in the Vegetable than in the Animal kingdom, is simply, that in the former the specialization of function is nowhere carried so far as in the latter; so that any part of the general surface of a plant can perform in a considerable degree all the functions of all the rest. We might then *à priori* expect, that whilst the roots are, in the usual condition of the perfect plant, the organs by which its fluid nutriment is absorbed, and the leaves its organs of transpiration and respiration, some traces of the primitive community of function enjoyed by the general surface of the simpler tribes, would be found in the capacity of each of these organs to perform in a certain degree, if required, the function of the other. Thus, it is evident that when the roots are either absent or imperfect, or are implanted in an arid or barren soil, serving merely to fix the stem (as happens with many *Orchideæ* and the generality of aerial parasites), the plant must derive its chief supply of nutriment through the absorption performed by the leaves, or, in leafless plants, (as the *Cacteæ*), through the general surface. And it must be obvious to all who have observed the manner in which plants, faded by the intense action of light and heat, are refreshed by the natural or artificial application of moisture, that absorption takes place, in these instances also, by the general surface, as well as by the roots.—Various experiments have been devised, with the view of determining the relative extent to which the plant is supplied by these two channels; but the proportion appears to depend upon the circumstances of its growth. Thus, Bonnet took some specimens of *Mercurialis*, and immersing the roots of part of them in water, he placed others so that only their leaves touched the fluid. A small shoot of each plant was kept from contact with water; and after the experiment had proceeded for five or six weeks, those which had derived all their nutriment through the leaves were nearly as vigorous as those which had imbibed it by the roots. It is by the under surface of the leaf, where the cuticle and cellular tissue beneath it are least compactly arranged, that absorption is performed with the greatest rapidity; and the downy hairs with which some plants are plentifully furnished, seem to contribute to this function, acting like so many rootlets. These prolongations of the surface are usually wanting in such plants as grow in damp shady situations, where moisture already exists in abundance; but in hot, dry, exposed localities, where it is necessary that the plant should avail itself of every means of collecting its food, we find the leaves thickly set with them; and this diversity may be observed in different individuals of the same species of plant, according to the soil and climate in which they exist, and even in the same individual if transplanted.

179. In tracing the gradual evolution of the special Absorbent apparatus of the more perfect Plants, we may observe many interesting relations between the progressive stages of its development, and the permanent forms of the same system in the lower orders. Thus, the embryo at its first appearance within the ovule (CHAP. XI.) is nothing but a single cell, like that of the *Protococcus*, in the midst of the store of semifluid nutriment prepared by its parent, which it gradually absorbs by its whole

surface, just as do the simplest Cellular plants. At the time of the ripening of the seed, we find a rudiment of the future root, which is developed during germination; but in the early stages of this process, the radicle simply prolongs itself into the ground, and appears to be equally capable of imbibing moisture through its whole length, like that of the Liverworts or Mosses. It is not until the true leaves are evolved, that the root begins to extend itself by ramification; then first protruding perfect fibrils, composed of woody fibre and vessels, and terminated by spongioles.—Thus, then, in the development of the Absorbent system of Vegetables, the first which we have been called upon to study in detail, we find a characteristic example of the laws which have been already enunciated (CHAPS. I., II.); for it has been shown that, whether we trace its various forms through the ascending scale of the different tribes of Plants, or watch the progress of its evolution in the more perfect orders, it is constantly to be observed that the *special* structure and function arise by a gradual change out of one more *general;* and that, even where the *special* organ is most highly developed, the *general* structure retains, in some degree, the primitive community of function which originally characterised it.

3. *Absorption in Animals.*

180. It has been shown in the preceding chapter, that the conditions under which the function of Absorption is performed in Animals, are so far different from those which obtain in Plants, that a preparatory process of *Digestion* becomes necessary in the former, for the reduction of the food to the fluid form required for its entrance into the system. This process is effected in cavities of the body, which are bounded by a continuation of its external surface, modified, by its secreting power, to supply the means necessary for the solution of the aliment, and, by its absorbent faculty, for the selection of the part of it capable of contributing to the nutrition of the fabric. But so long as this aliment remains unabsorbed, it cannot be regarded as introduced into the system; since it merely holds the same relation to the absorbent vessels, that the nutritious fluid in which the roots of plants may be immersed, bears to the ducts which they enclose. This is brought into clear view by the remarkable fact, that the poison of the most venomous Serpents, and the Woorara-poison of the South American Indians, of either of which a very small quantity will produce death when it is introduced by the minutest puncture or scratch into the current of the circulating fluid, are perfectly innocuous when taken into the stomach; the mucous membrane of the alimentary canal apparently having a peculiar inaptitude for allowing them to penetrate by imbibition, either into the blood-vessels or into the absorbents. Some experiments recently made upon the latter substance, by MM. Bernard and Pelouze, are peculiarly interesting, as confirming the statement already made (§ 176), that the absorption of particular substances, however favourable their condition may appear, may be prevented by the simply-physical conditions of the membrane which they have to traverse.*

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* That the absence of poisonous effects from the *Woorara* poison, when it is simply introduced into the stomach, does not arise from any modification effected in its properties by the agency of the gastric juice, is shown by the fact that the poison, after digestion in

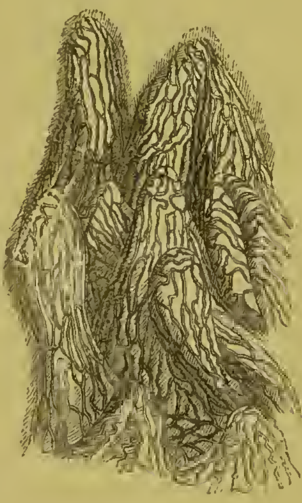
181. It has further been shown that the introduction of the nutritive material into the system, is effected in the lowest animals by simple imbibition into the tissues that surround the digestive cavity, and by percolation through them towards the more remote parts; and where such is the case, the digestive cavity either itself occupies a very large part of the body, as in the Hydroid Polypes (§ 151), or prolongations of it, in the form of canals, extend to the parts remote from the principal cavity, as in many of the Acalephæ (§ 153). In most other Invertebrata, the nutritive materials are taken-up, not directly from the digestive sac, but from the visceral cavity in which it lies. Into this visceral cavity they freely pass, by the apertures that remain patent in the Actiniform and Alcyonian polypes (§ 152); but in all the higher forms of the digestive apparatus, the passage takes place only by transudation through the walls of the stomach and intestinal tube; the *chyle*, or incipient blood, being thus filtered-off (so to speak) from the *chyme*, or primary product of digestion. In the lowest Mollusca (Fig. 49) as in Rotifera (Fig. 96), and certain Crustaceans (Fig. 105), the flux and reflux of this chylous fluid through the body constitute the only means by which its tissues are supplied with nutriment; and even in the higher Mollusca, Insects, and Crustacea, the sanguiferous system is in such free communication with the visceral cavity, that their blood cannot be differentiated from its contents. There is in these animals, therefore, no other special *absorption*, than that which takes place through the walls of the alimentary canal. But in the Echinodermata and Annelida, which have a closed sanguiferous system, the contents of this must be taken-up, either from the visceral cavity (which still appears to be the principal channel for the transmission of *nutritive* materials through the body, their sanguiferous circulation being in all probability chiefly subservient to *respiration*) or directly from the alimentary canal. That absorption does take place in this latter mode, would seem probable from the very minute distribution of blood-vessels upon the surface of the intestinal

that fluid for 24 or 48 hours, remains as virulent as ever; whilst the gastric fluid to which Woorara has been added, loses none of its solvent power. The various secretions which make-up the intestinal juices, have been experimented-on with the same results. Hence it appears that the cause of the innocuousness of the poison, under these circumstances, must be looked-for in the gastro-intestinal mucous membrane, which will not give passage to the active principle of the poison, soluble as this is. Experiment proves this to be the case. If the gastric mucous membrane of a recently-killed animal be adapted to an endosmometer, so that the mucous surface looks outward, and the endosmometer containing sugared water is then placed in a watery solution of woorara, endosmose will have been found to have taken place in three or four hours, for the liquid will have risen in the tube; and yet this will contain no trace of woorara, as may be ascertained by inoculating with it. If the experiment were allowed to go on for a much longer time, the endosmosis of the poison might occur; but we should then find that the mucous membrane had undergone modification, the mucus and epithelium covering it being altered, so that imbibition and endosmosis of the woorara becomes possible; and if, in place of taking a quite fresh mucous membrane, we take one that has undergone some change, the endosmosis of the poisonous fluid occurs instantly.—As it was interesting to ascertain whether other mucous membranes possessed this resisting power, those of the bladder, nasal fossæ, and eyes were tried, and constantly with the same results. An injection was retained in the bladder without inconvenience, for from six to eight hours, by a dog; but the urine it passed after this time had all the toxical properties of woorara. One mucous membrane alone, the pulmonary, is excepted from this immunity; for the poison, when applied to it, produces the same effects as when introduced into the subcutaneous areolar tissue.—"L'Union Médicale," 1850, No. 125.

tube, which will be shown to exist in the Holothuria (Fig. 40) and in many Annelida (Figs. 114, 115).

182. In the Vertebrata, however, it is by *vessels* alone, that the nutritive fluid is removed from the alimentary canal, the walls of which do not allow it to transude into the surrounding cavity. And we here find provided, in addition to the blood-vessels that are copiously distributed upon the coats of the gastro-intestinal tube, a special set of *Absorbent* vessels, which seem to be destined, not only for the introduction of *nutritive* materials into the system, but also for submitting these to a certain preparation (CHAP. VIII.), before they are admitted into the current of the circulation. The 'Absorbent system' of vessels consists of two principal divisions, which may be compared to two sets of roots proceeding from a common trunk; one of these commences upon the walls of the intestines, and is termed the 'Lacteal' system, from the milky character of the 'chyle' which it contains; whilst the other takes its origin in various parts of the substance of the organism at large, especially in the skin and subcutaneous textures, and is known as the 'Lymphatic' system, from the transparent watery aspect of the liquid it conveys.—Although the walls of the whole gastro-intestinal canal are furnished with Absorbent vessels, in common with other membranous surfaces, yet it is on those of small intestine, below the point at which the liver and pancreas discharge their secretions, that the *Lacteals* especially abound; and they seem, in the higher Vertebrata at least, most commonly to originate in the interior of the villi, where they are surrounded by the plexus of capillary blood-vessels that lies immediately beneath the external surface of these filamentous processes (Fig. 108). In Fishes, however, the villi are few, or are altogether absent, and the lacteal trunks receive their supplies through a coarse plexus situated in the walls of the intestinal canal. Such a plexus is seen also in Reptiles, in which villi are developed; and it seems probable that it exists in the higher Vertebrata, in which the mucous membrane is much more thickly set with villi, and in which it appears to be chiefly through the lacteals contained in these, that the chyle gains admission into the larger trunks. The precise mode in which the lacteals commence near the free extremities of the villi, cannot be stated with certainty; but it is probable that they form loops by anastomosis with each other, so that there is no proper free extremity in any case. It is beyond all doubt, however, that the lacteals never commence by orifices upon the internal surface of the intestine, as was formerly imagined. When these vessels are turgid with chyle, the extremity of each appears to be imbedded in a collection of globules, presenting an opalescent appearance, which give to the end of the villus a mulberry-like form; and this appearance is due to the distention of the epithelial cells covering the extremities of the villi, with the oleaginous chyle which they have absorbed, and which they

FIG. 108.



Villi of Human Intestine.

afterwards yield-up to the lacteals, returning to their original condition when this *selective* operation has been accomplished.[*]

183. The *Lymphatic* vessels are distributed in the greater number of tissues and organs which possess vessels for the conveyance of blood; but to this general statement, there are some remarkable exceptions; for they are entirely wanting in the substance of the brain and spinal cord, although they are found in their investing membranes; and they occur very scantily in the muscles. It appears to be in the skin and the subcutaneous textures, at least in Man, that they are most plentifully distributed; and they seem there to originate, like the lacteals of the intestinal walls, in plexuses of which the meshes are very close. According to Prof. Kölliker, the lymphatics in the tail of the Tadpole do not form a network, but branch out like rootlets, their ultimate extremities, or rather their commencing radicles, having free but closed ends, running out into fine points;[†] it may be doubted, however, whether this is not the result of a want of completeness in their development, and whether these ramifications would not meet and inosculate in the fully-developed Frog. Like the capillary blood-vessels (§ 211), they take their origin in stellate cells, which send forth long projections; but these branches do not inosculate with each other in any other way than to form continuous tubes; and if they subsequently constitute a plexus, it must be by the development of connecting arches at a later period.—It has been maintained that the minute lymphatics communicate with the capillary vessels in their neighbourhood; and these communications have been supposed by some to allow the direct transmission of the lymph into the sanguiferous system; whilst by others it has been inferred that the *liquor sanguinis*, or fluid portion of the blood, (which, when diluted, closely resembles the contents of the lymphatics in its composition) finds its way into the absorbents. It is nearly certain, however, that no such apertures exist; and that when any direct passage of fluid does take place from one set of vessels into the other (as is often the case in artificial injections, and was noticed by Prof. Kölliker in watching the circulation in the tail of a Tadpole which had been injured), it is through an abnormal opening.

184. The walls of the absorbent vessels (whether lacteals or lymphatics) are extremely thin, so that the character of their contained fluid can be readily discerned through them. Those which form the ultimate ramifications of the system, appear to be limited only by a very delicate homogeneous membrane; and it is not certain that even this is universally present in the absorbents of Fishes. A similar membrane, covered with a layer of pavement-epithelium upon its inner or free surface, constitutes the lining of the mid-sized and larger trunks; but these possess, in addition, a middle or fibrous layer, in which non-striated muscular fibres may be distinguished, and an external sheath of areolar

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[*] By Prof. Goodsir, who was the first to direct attention to the peculiar appearance presented by the cells at the extremities of the villi during the process of lacteal absorption, it was maintained that the ordinary epithelial cells fall-off, and that the chyliferous cells are developed *de novo* within the villus, that is, beneath its basement-membrane. The researches of several excellent observers, however, have shown this view to be erroneous, and have established that stated in the text. (See especially Prof. Kölliker's "Mikroskopische Anatomie," Band ii. § 169.)

[†] "Annales des Sciences Naturelles," 3^e Sér., Zool., Tom. VI., p. 98.

tissue. In the higher Vertebrata, the Absorbents are furnished with valves, which allow the passage of their contents in only one direction, namely, from their origin towards their termination in the sanguiferous system; these valves, however, seem to be wanting in the 'plexuses of origin,' which are filled by mercury injected into any part of them. In Fishes and Reptiles, however, in which this system is obviously developed upon an inferior type, the valves are few or are altogether wanting.—In the higher Vertebrata, again, certain small solid bodies are found in the course of the lacteals and lymphatics, which are termed 'absorbent glands.' The structure of these, however, does not correspond with that of ordinary *glands;* and they have been more appropriately named 'ganglia,' for they are essentially composed of plexuses of absorbent vessels, convoluted (so to speak) into knots, and dilated into larger cavities, amongst which capillary blood-vessels are minutely distributed; the whole being bound together by areolar tissue and invested in a capsule of the same. These blood-vessels have no direct communication with the interior of the lacteals, but are separated from them by the membranous walls of both sets of tubes; so that whatever passage of fluid normally takes place from one set of vessels to the other, must be accomplished by transudation through these.* According to the observations of Prof. Goodsir, the absorbents, when they enter a gland, lay aside all but their internal coat and epithelium; and the latter, in place of retaining its pavement-like character, presents itself as an irregular layer of spherical nucleated corpuscles, measuring about 1-5000th of an inch in diameter; which layer is thickest in the dilated lymphatics which form the 'cells' of the centre of the gland, and becomes gradually thinner towards the periphery, where it is continuous with the epithelium of the afferent and efferent vessels. The inner layers of the central epithelium appear to have no tenacity; so that the component cells may be readily detached from one another, and carried-off in the fluids which traverse the cavity.—Having thus considered the general structure of the Absorbent system, we shall proceed to notice its more special peculiarities in the different classes of Vertebrata.

185. The proper Absorbent system is exhibited in its simplest and most diffused form in *Fishes*, the lowest class in which its existence has been demonstrated. Where it consists of distinct vessels, their walls are very thin and distensible. The Lacteals commence in a somewhat coarse network of canals, that seem channelled-out (as it were) beneath the mucous lining of the intestinal canal, and cannot be shown to possess definite walls; from these, however, the chyle is conveyed away by proper vessels, which form capacious plexuses in the mesentery, along the course of the alimentary canal. The Lymphatics are distributed extensively through both the superficial and the deep-seated parts of the body; and, they also, by the convolutions and anastomoses of their trunks, form numerous plexuses in various situations, especially around the veins, which may be regarded as the first indications of the so-called

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* It has been asserted by many anatomists, that free apertures exist, by which the contents of one set of vessels can pass directly into the other; but these statements are founded on the results of injections, which can be very easily *forced to make* such apertures; and the most careful examination has failed to detect them, when no such procedure has been employed.

'glands' that are presented in the higher classes. Some of these trunks, moreover, dilate into sinuses, which appear to be contractile, and prefigure the 'lymphatic hearts' of Reptiles. Such a sinus may be seen in the tail of the Eel; and another is found on each side of the cranial cavity of many Fishes, externally to the jugular veins. Although a considerable proportion of the lymphatic trunks unite with the lacteal vessels, to form principal canals (corresponding with the thoracic duct in higher animals), which empty their contents into the systemic veins near the heart, there are many other communications between the two systems, as Fohmann appears to have satisfactorily demonstrated. Thus, the caudal sinus of the Eel discharges its contents into the caudal vein, the orifice being provided with a valve.

185. The conformation of the Absorbent system presents several interesting peculiarities in the class of *Reptiles*. As in Fishes, the vessels are generally destitute of valves, though these may occasionally be observed in the larger trunks; but they everywhere seem to possess distinct walls. When compared with that of Birds and Mammals, the absorbent system of Reptiles seems to possess an enormous extension; large and capacious lymphatic plexuses being developed around the great veins, and the length of the trunks being often augmented by doublings and convolutions. But this extension is rather apparent than real; for there is still an absence of the 'glands,' which seem to concentrate, as it were, the assimilating power of a long series of tubes; and the relation of the Absorbent system of Reptiles to the more concentrated apparatus of Birds or Mammals, thus comes to resemble that which the extended tracheal system of the Insect bears to the lungs of the higher Vertebrata.—The *Lacteals* in Reptiles, as in the classes above them, partly commence in the 'villi' of the intestinal canal; but, as in Fishes, there is also a very coarse plexus of absorbents beneath its mucous lining. The fluid which they absorb is collected into a *receptaculum chyli*, situated at the root of the mesentery; and from this it passes by two or more ducts, which also receive many of the lymphatic trunks, into the great systemic veins. The *Lymphatic* portion of the system is furnished, in most Reptiles, with certain pulsating dilatations, or *lymphatic hearts*, which aid in the propulsion of the contents of the vessels; the walls of these contractile cavities are formed of striated muscular fibres. In the *Frog* there are two pairs of them; one situated just under the skin, through which its pulsations are readily seen in the living animal, immediately behind the hip-joint; while the other pair is more deeply seated at the upper part of the chest. The former receive lymph from the posterior part of the body, and pour it into the veins proceeding from the same part, by orifices furnished with valves; the latter collect that which is transmitted from the anterior part of the body and head, and empty their contents in like manner into the jugular vein. Their pulsations are totally independent of the heart and of the acts of respiration, since they continue after the removal of the former, and for an hour or two after somatic death and the complete dismemberment of the animal. Neither are they synchronous with each other on the two sides of the body, nor always performed in the same space of time; for the pulsations are not only generally irregular, but sometimes exhibit long and frequent intermissions; when in constant action, they occur about sixty times in a

minute. From the observations of Volkmann, however, it appears that these movements are dependent upon the connection of the lymphatic hearts with the corresponding segments of the spinal cord; since they cease when these are destroyed, although all other parts may be left uninjured; while they continue so long as this connection remains perfect, although all other parts of the nervous centres be destroyed.*—A pair of vesicles similar to the posterior pair in the Frog, has been detected in *Salamanders*, *Lizards*, and *Crocodiles*, in which they are situated near the root of the tail, and are connected, in like manner, with the veins of the lower extremity; they have also been discovered in *Serpents*, where they lie under the last rib. It was for some time believed that the *Chelonia* formed an exception to the general fact of the existence of such pulsating receptacles in Reptiles; but these have been shown by Müller to be particularly large in that group, in which they lie behind the superior extremity of the iliac bones, receiving the lymph by capacious trunks from the posterior extremities, and pouring it into veins that discharge themselves into the reno-portal system.†

186. In *Birds*, we find the Absorbent system existing in a more perfect form; its trunks being everywhere provided with valves, and the diffused plexuses being partly replaced by 'glands' or 'ganglia,' which may be probably considered as performing the same function by an organisation of more concentrated character. The *lacteals*, which are not furnished with these glands, all converge towards a *receptaculum chyli*, from which proceed two thoracic ducts, one on either side, to terminate in the angles formed by the junction of the jugular and subclavian veins. These ducts receive, also, most of the lymphatic trunks; but the lymphatic system has two other communications, as in Reptiles, with the veins of the lower extremity. These are connected with two large dilatations of the lymphatic trunks, which are evidently analogous to the lymphatic hearts of Reptiles, but which do not seem to have any power of spontaneous movement. In the Goose, they are about the shape and size of a kidney-bean, and are situated in the angle between the tail and the thigh. They were supposed by Panizza to possess an automatic power of alternate contraction and dilatation; but these motions have been shown by Müller to be due to the respiratory actions,—being synchronous with them, and ceasing when they are interrupted.

187. In the Absorbent system of *Mammalia*, we witness its most concentrated and highly-developed form. The vessels are copiously provided with valves; and their parietes are firmer than in the lower classes. Instead of the extensive plexuses of Fish, we find small dense 'glands' disposed in different parts of the system; these are more numerous than in Birds, and present themselves on the lacteals as well as on the lymphatics, being known in the one case as the 'mesenteric,' and in the other as 'lymphatic' glands. In some Mammalia, especially of the order *Carnivora*, the mesenteric glands cluster together into a single mass, named the *pancreas Asellii*, which lies at the root of the mesentery. The Lacteals all discharge their contents into the *receptaculum chyli*, which is situated in the lumbar region, close to the spine; into the same receptacle, many Lymphatic trunks pour the fluid which they have collected

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* "Muller's Archiv.," 1844. † Ibid. 1840.

from the posterior part of the trunk and extremities; and from it arises the *Thoracic Duct* of the left side, which passes forwards along the spine, receiving other lymphatic trunks in its course, and terminates at the junction of the left jugular and subclavian veins. A smaller trunk on the right side receives the lymphatics of the right side of the head and upper extremity, with those of the right lung and right side of the liver; and this terminates, in like manner, at the junction of the right subclavian and jugular veins. It is a beautiful instance of mechanical adaptation, that as the angle formed by the convergence of two veins is a point of much less resistance than any other part of the walls of the vessels, the easiest possible entrance is thus provided for the fluid discharged from the thoracic ducts into the current of the circulation. Although these are the only two canals by which the Absorbents usually communicate with the veins in Man, their number is greater in many species of Mammalia; they all terminate, however, in the same part of the venous system. Thus, the left thoracic duct often resembles rather a plexus of vessels than a single tube; branches proceeding from it and then reuniting, and at last terminating in the veins by several apertures. Sometimes it consists throughout of two tubes, which anastomose with each other and with the duct on the right side, and terminate separately in the veins; and in the Pig a branch of communication is sent off to the vena azygos, which is a small trunk running in proximity with it along the spinal column. All these modes of distribution occur as irregularities of conformation in the Human subject, the former not being uncommon; the last, however, is rare.

188. The cause of the onward movement of the contents of the Absorbent vessels in the higher Vertebrata which have no 'lymphatic hearts,' and also of the flow of fluid towards these pulsating cavities in the animals which possess them (situated, as they are, close to the points where the fluid of the absorbents is discharged into the veins), has not been positively determined. This movement may be partly attributed to the *vis à tergo*, produced by the continual imbibition of fresh fluid into the rootlets (so to speak) of the vascular tree, and partly to rhythmical contractions (with alternating dilatations) of the villi themselves, as observed by MM. Gruby and Delafond;* and although it may be thought, from the extreme distensibility of the walls of the absorbents, that such forces will be rather expended in dilating *them*, than in pushing onwards the column of liquid which they contain, yet it must be remembered that they are surrounded by tissues, whose tonicity, during the living state, gives to them much more resisting power than they possess after death. Further, in all the movable parts of the body, assistance is doubtless afforded by the occcasional pressure which will be exercised upon the absorbents by the surrounding tissues; for while this pressure is operating, it will tend to empty them of their contents, which are only permitted by their valves to pass in one direction; and when the pressure is relaxed, they will be re-filled from behind. But it seems probable that the regular propulsion of the fluid mainly depends upon an alternate contraction and dilatation of successive portions of the vessels, slowly repeated at intervals; such alternations having been witnessed by Prof. Kölliker in the tail of the

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* "Comptes Rendus," 1842, p. 1199, and 1843, p. 1195.

tadpole; and it being apparently by such contraction, without subsequent dilatation and re-filling, that the absorbents are emptied after death, and this with considerable rapidity.

189. We have now to enquire into the relative parts which are performed in the function of *Absorption*, by the proper Absorbents, and by the Blood-vessels; and although these cannot yet be said to be precisely definable, yet there can be little doubt that we are in possession of the general truth with regard to them.—From the time when the Lacteal vessels were first discovered, down to a comparatively recent period, it was supposed that they constitute the channel through which *all* fresh nutritive material is taken into the body; and this idea seemed to derive confirmation from the great uniformity in the composition of the chyle, which, though different as a whole from that of blood, appeared adequate to supply those substances to the latter, which are most constantly being eliminated from it by the nutritive and respiratory operations. Various considerations, however, would lead to the conclusion, that the nutritive materials do not enter through the lacteals alone; but that the most soluble portions of them, together with other substances not nutritious, find their way directly into the blood-vessels.—In the Invertebrata, it will be recollected, no special Absorbent system exists; and in all those which possess blood-vessels, it is by them alone that alimentary matters are introduced into the system; it would not seem likely, therefore, that this most general method of performing the function should be entirely superseded in Vertebrata by the more special one. But further, when the extraordinary vascularity of the whole gastro-intestinal membrane is considered, together with the peculiarity of the special distribution of the capillaries in the villi; and when it is remembered also that the rapid movement of blood through these, creates the condition most especially favourable to the passage of liquids into them from the outside (§ 172), it might be almost certainly affirmed that endosmose *must* take place between the contents of the alimentary canal and the blood in the vessels. —This conclusion has been confirmed by numerous experiments. Thus it was ascertained by MM. Tiedemann and Gmelin, that when various substances were mingled with the food, which might be easily detected by their colour, odour, or chemical properties,—such as gamboge, madder, camphor, musk, asafœtida, and various saline substances,—they were seldom found in the chyle, though many of them were detected in the blood, and some had even passed into the urine. So, again, it was found that if any of these substances be introduced into a portion of the intestine separated by ligatures from the remainder, and all the vessels of that portion be divided or tied, save its artery and vein, the substance may speedily be detected in the blood, and if it be poisonous its effects are manifested nearly as soon as usual; whilst, if the blood-vessels be tied, the lacteals being left entire and uninterrupted, a long period elapses before there is any evidence of absorption. It cannot be doubted, then, that alimentary substances in a state of solution, such as albumen, gelatine, or sugar, may pass into the blood-vessels by simple endosmose, when the relative densities of the blood and of the intestinal liquids are such as to favour the inward current. Conversely, it might be inferred that if the liquid in the intestines be of a nature to determine the endosmotic current in the contrary direction, some of the constituents of the

blood would be drawn from them into the alimentary canal. Now it has been shown by the experiments of Poisseuille, that an endosmotic current takes place through animal membranes *from* the serum of the blood towards certain saline solutions; and thus it happens that when these are taken into the alimentary canal, they produce a copious exudation of fluid from its walls, which fluid contains a considerable quantity of albumen.—It appears, then, that an interchange between the contents of the blood-vessels and those of the alimentary canal takes place, in either direction, in a manner which is in all respects conformable to physical principles; so that Absorption must be effected through the blood-vessels of the higher animals, as of the lower.

190. On the other hand, the Lacteals, as already pointed out, would appear to receive only substances of a particular class, more especially fatty matters in a state of more or less fine division, with which albuminous compounds are intimately mixed. These, being first drawn-in by the epithelial cells at the extremities of the villi (§ 182), and then transferred to the lacteals, are doubtless obtained directly from the food; for the quality of the Chyle depends upon that of the aliment last digested, it being of an opaque white if that food contained much oily or fatty matter, and of a more transparent aspect if such matters were deficient. Moreover, the experiments of Bouchardat and Sandras* have shown, that particular kinds of fatty substances with which animals may have been fed, are recognisable in the chyle; and on the whole it may be considered, that the special function of the lacteals is to take up the oleaginous portion of the food, and to bring it into that intimate relation with albumen which seems to be requisite for its subsequent assimilation (CHAP. VIII.) Still it appears by no means certain that the blood-vessels also may not absorb oleaginous substances, as they do in Invertebrated animals; particularly as it has been shown by the experiments of Prof. Matteucci,† that if an emulsion be made by shaking a few drops of oil in water to which a little alkali has been added, and an endosmometer filled with a weak alkaline solution be then immersed in this emulsion, the oil penetrates in a short time through the membranous partition, and makes its appearance in the interior of the endosmometer. Now as the blood is slightly alkaline, and as its density favours the imbibition of fluid, there seems no reason why fatty matters should not thus find their way into the blood-vessels, when they have been reduced to a state of fine division in the alimentary canal, and have been rendered alkaline by the admixture of the biliary and pancreatic fluids.

191. With regard to the relative share taken by the Lymphatics and the Blood-vessels, in the absorption of fluids by the external surface or from the closed cavities of the body, and in that 'interstitial' absorption which removes the solid particles of the fabric when they no longer retain their vital endowments, there has been a yet greater amount of misapprehension. It was long imagined (the doctrine having been strongly sustained by John Hunter and his immediate followers), that the office of the Lymphatic system is to take-up and remove all the *effete* matter which is to be cast out of the body, as no longer adapted to form part of

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* "Annales des Sciences Naturelles," 2e Sér., Zool., Tom. XVIII., XX.

† "Lectures on the Physical Phenomena of Life," Dr. Pereira's Translation, p. 111.

it, and as inconvertible into any other useful product. For such an idea, however, there is not the least adequate foundation. The liquid contained in the lymphatics has all the characters of dilute 'liquor sanguinis' (the liquid portion of the blood in which the corpuscles float); and it differs from that of the lacteals chiefly in the absence of fat. The lacteals, indeed, when the alimentary canal is empty, seem to perform the function of lymphatics; being found to contain a fluid which resembles lymph in every respect, and is probably derived from the same source. Again, as the lymphatics do not discharge their contents into any of the outlets through which they might be carried off, or convey them to the excretory glands by which they might be eliminated under some other form, but pour them into the same receptacle with the nutrient materials newly imbibed from the food, whence both are propelled together into the general current of the circulation, it seems almost certain that their contents, in whatever mode obtained, are destined to be employed in the formation of the tissues, and not to be forthwith eliminated from the system.

192. With respect to the source of the Lymph, and the manner in which it is imbibed, there is at present a deficiency of accurate knowledge. It is very probable, however, that it partly consists of the residual fluid, which, having escaped from the blood-vessels into the tissues, has furnished the latter with the materials of their nutrition, and is now to be returned to the current of the circulation. But it also seems not unlikely, that it may partly be derived from those particles of the solid framework, which have lost their vital powers, and are therefore unfit to be retained as components of the living system, but which have not undergone such a degree of decay, as to prevent them from serving, like the aliment derived from the dead bodies of *other* animals, as a material for reconstruction, when it has been again subjected to the assimilating process.* In what way the *selective* power is exercised, by which extraneous substances are usually prevented from entering the lymphatic system, when they are quickly received into the blood-vessels, cannot at present be even guessed-at: since there is no reason to believe that the lymphatic 'plexuses of origin' are in relation with cells (like those of the villi) to which such a function might be attributed.—Although the rule is not so constant for the lymphatics as for the lacteals, yet it does not appear that these absorbents readily take up liquids in contact with the skin, unless they be of an alimentary character, assimilating in composition to lymph. There are certain saline compounds, however, which seem to pass as readily into the lymphatics, when applied in solution to the cutaneous surface, as into the blood-vessels, or even more readily; no general rule, however, can be laid-down upon this subject; and it is probable that differences in the relative distribution of the two orders of vessels in the skins of different animals, may considerably influence the result. A peculiar aptitude of the lymphatics for the absorption of

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* In this point of view, the almost entire absence of lymphatics from the Muscular and Nervous tissues presents an obvious signification; since when *these* tissues are disintegrated by being called into vital activity, their elements at once pass into new states of combination, which, being purely excrementitious in their character, are not fit to be received into the lymphatic system for the purposes of nutrition, but are directly conveyed by the sanguiferous current to the organs which are charged with their elimination from the body.

milk seems to be shown by the experiments of Schreger, who found that the lymphatics of a limb long immersed in it became turgid with this fluid: that none of it could be detected, however, in blood drawn from the part, was sufficiently accounted-for by the circumstance that a bandage had been tied round the limb, thereby producing turgescence of the superficial veins. The fact that the lymphatics in the neighbourhood of collections of peculiar animal fluids, sometimes become filled with those fluids,—as bile from an over-distended gall-bladder, or pus from an abscess, —need not be regarded as invalidating the general statement already made with regard to their probable function; for there can be no doubt that under such circumstances a direct entrance might be readily gained into the absorbents, either through rupture or ulceration of their walls; and in this way alone could particles so large as pus-globules find their way into these vessels. The case is different, however, with regard to substances introduced through the skin by friction; for these often seem to find their way quickly into the lymphatics, as is shown by the circumstance that if they be of an irritating character, red streaks appear along the course of the absorbents, and the neighbouring glands are swollen. This is probably to be explained by the peculiarly abundant distribution of the lymphatics in the skin, and the ready access which liquids can obtain to their walls.

193. There can be no reasonable doubt that it is by the Blood-vessels, rather than by the Lymphatics, that all that 'interstitial' and 'superficial' absorption is performed, which is not of a directly nutritive character; and in particular that those effete matters are carried away from the tissues, which are destined to immediate elimination. Thus, the most rapid and constant in its formation of all the excretory products, and the most injurious if retained, is carbonic acid; and this is conveyed by the venous system to the Lungs, in which it is forthwith removed from the blood. So again, it is by a special arrangement of a part of the venous system, that the Liver is supplied with venous blood for the elaboration of bile; indicating that it is in such blood that the elements of the bile most abound. And this will be seen to be the case with regard to the Kidneys also, in the lower Vertebrata; although in the higher, it is from the arterial system that they receive their supply of blood for secretion as well as for nutrition. Further, as no lymphatics exist in the whole Invertebrated series, it is obvious that nothing but the sanguiferous system can perform the entire function of interstitial absorption; and the same must be the case in those tissues of Vertebrata, which are destitute of special absorbents. Experiments demonstrating the exercise of the absorbent power by the blood-vessels, upon substances placed in contact with them, are most numerous and convincing; it will be sufficient to mention two. Mayer, having injected a solution of prussiate of potash into the lungs, detected it in the left cavities of the heart sooner than in the right; whence it is obvious that it must have been absorbed by the pulmonary blood-vessels more speedily than by the lymphatics of the lungs. And when the jugular vein of a young dog was laid bare by Magendie, and a solution of nux vomica was supplied to its external surface, the symptoms of poisoning manifested themselves in four minutes.

194. It may be stated, then, as a general fact, that the Blood-vessels

are the principal channels, through which water and substances dissolved in it are introduced into the body, either from the walls of the alimentary canal, or from the general surface; and by which that interstitial absorption is effected, whereby the particles that have served their purpose in the solid fabric are removed from it:—But that the Absorbent system, possessed by the higher animals, is the special channel for the introduction of oleaginous matters, suspended in an albuminous fluid, from the intestinal tube; and for the return to the sanguineous circulation of such matters as may be yielded-back by the tissues (whether from the superfluity imparted to them by the blood, or as products of their own disintegration), in a state to be again employed for the purposes of nutrition. We shall hereafter find reason to believe (CHAP. IX.), that during its slow movement through the absorbents, and especially during its passage through their glandulæ, the Chyle and Lymph undergo changes by which it is brought into a nearer likeness to the Blood, more especially in regard to the vital properties of that fluid.

195. Notwithstanding that it is through the walls of the alimentary canal, in most of the higher animals, that the introduction of nutriment from without is chiefly effected, yet it must not be lost sight of that the *general surface* of Animals, as of Plants, is still to a certain degree capable of taking this function upon itself; and this not merely when the regular channels have been closed, but even in some cases as the regular functional duty of that part. Thus the experiments of Dr. Madden* show, that a positive increase usually takes place in the weight of a man immersed in a warm-bath, even though there be at the same time a loss of weight by pulmonary exhalation and by transudation through the skin; and he found that when this loss was taken into account, the quantity of water absorbed was about an ounce and a half in half an hour. The absorption will be more rapid, when the fluids of the body have been previously diminished by unusual exhalation; thus Dr. S. Smith mentions that a man who had lost nearly three pounds by perspiration during an hour and a quarter's labour in a very hot dry atmosphere, regained *eight ounces* by immersion in a warm bath for half an hour. And a patient into whose stomach no aliment of any kind could be introduced, has been kept alive for some time chiefly by cutaneous absorption, the body having been immersed night and morning in a bath of milk and water, and imbibing from 24 to 36 ounces per diem.—Even the vapour of the atmosphere may, in certain cases, afford the requisite supply. Thus *Frogs* seldom or never drink, but they habitually live in a moist atmosphere; and when they have lost fluid by exposure to hot dry air, they will regain their weight by being left for a time upon moist sand, and the bladder (which serves as a reservoir of water for cutaneous exhalation) though previously emptied, will be refilled.† It is probable that the same may occur in all animals with a soft naked skin; and there are cases which (if the facts be correctly reported) would seem to prove unequivocally, that the cutaneous and pulmonary surfaces even in Man may serve upon occasion for the introduction of large quantities of fluid from the vapour of the atmosphere.‡

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* "Prize Essay on Cutaneous Absorption," pp. 59—63.

† See Art. 'Amphibia' in "Cyclop. of Anat. and Physiol.," Vol. i. p. 104.

‡ See the Author's "Human Physiology," §§ 468—470, and the cases there cited.

CHAPTER V.

OF THE CIRCULATION OF NUTRITIVE FLUID.

1. *General Considerations.*

196. In beings of the most simple organisation, whether belonging to the Animal or to the Vegetable kingdom, we have seen that every part of the surface is equally capable of absorbing the liquid aliment brought into contact with it; and that the materials of the tissues are supplied by the continual imbibition of the nutriment thus immediately derived from external sources. In such, therefore, it might be inferred that no transmission of fluid from one portion to another would be required for the purposes of the economy; and we find no evidence of its existence, either in a structure specially adapted to it, or in any visible motion of such fluid. But as, in more complex organisms, a small part only of the surface is particularly appropriated to the function of Absorption, it becomes evidently necessary that means should exist, for conveying to distant parts the nutriment they require. This is effected by the *Circulation* of the nutritious fluid, through a system of vessels or passages adapted to this purpose; and it may be regarded as a general statement of the condition of this system in all classes of living beings, that *its development is proportional to the degree of limitation of the power of absorption*, by which the parts directly imbibing aliment are removed from those requiring supplies.—But the conveyance of nutrient fluid to the remote parts of the organism, is not the only object to be fulfilled by the circulating apparatus; since the crude aliment must be exposed to the influence of the air before it becomes fit for its ultimate purpose, and that which has once passed through the tissues of Animals must undergo a similar process to restore it to its proper condition. This process, which constitutes the function of Respiration (CHAP. VI.), requires that the circulating fluid should pass, in all highly-developed organisms, through certain organs specially adapted for its performance; and hence the arrangement of the circulating system is modified, not only for conveying the alimentary materials from the part of the system where they are introduced to that where they are required, but also for causing it to be brought, during some part of its transit, into relation with the atmosphere. It is very evident, therefore, that the uninterrupted performance of this function is essential to the continuance of life: since not only does the nutrition of the tissues, or 'vegetative life,' wholly depend upon the materials thus supplied; but the presence of oxygen conveyed by the vital fluid is necessary for the active performance of the 'animal functions' by the nervo-muscular apparatus (§ 93).

197. In the study of the Circulation, we shall have reason to see the peculiar advantage to be derived from the investigation of the simplest conditions under which it may be performed. It has been from the confinement of their attention to this function, as it exists in the higher Animals only, that many Physiologists have adopted incorrect and narrow

views as to the powers by which it is maintained;—views which are incapable of extension to the whole Animal kingdom, far less to the Vegetable creation, and which must therefore be fundamentally erroneous. We shall endeavour to show that principles of wider comprehensiveness may be attained, by comparing the principal facts relative to the circulation of nutrient fluid, derived from *all* the classes of living beings in which it presents itself.

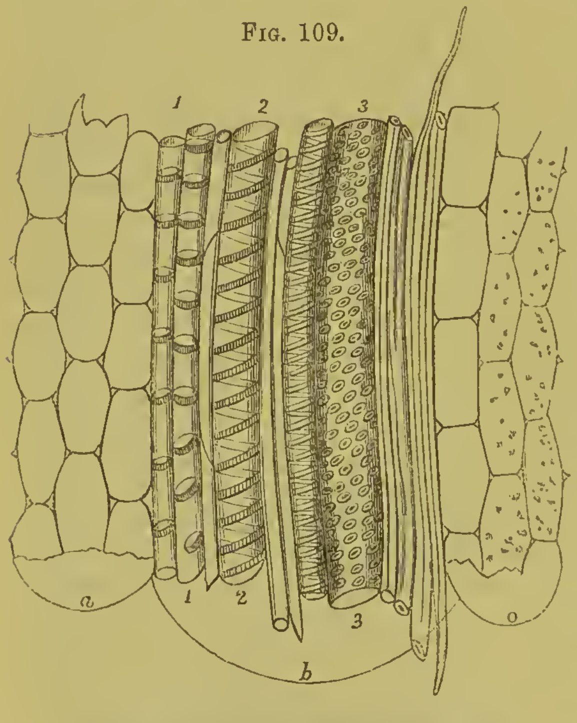
2. *Circulation in Vegetables.*

198. The tissues of the lower tribes of *Cryptogamia*, being almost entirely *cellular* in their structure, do not seem to be adapted for any very regular or definite transmission of fluid. The *Algæ*, as already stated, absorb by their whole surface; and there appears to be so little communication in this class between different parts of the same individual, that, if one portion be suspended out of the water, it will dry up and die, whilst that which remains immersed will preserve its freshness. No trace of vessels is discoverable in this order; the cells present a rounded form in almost every part; and the only deviation from this arrangement occurs in the 'veins' which strengthen the foliaceous expansions of some of the higher species, in which we find the cells somewhat elongated, and presenting an approach in form to woody fibre.—Amongst the *Lichens*, a similar uniformity of structure prevails; no appearance of vessels is perceptible; but wherever the form of a stem is assumed, the cells, which are rounded in the foliaceous expansions, possess more or less of elongation. As in this tribe the power of absorption is usually restricted to the side least exposed to light, some capability of diffusing the nutrient fluid is required; and it appears that, when the absorbent surface is placed in water, the liquid is slowly transmitted in the course of the elongated cells, to the whole plant.—In the higher *Fungi*, we may trace a further development of this simple form of the Circulating apparatus. In those species whose reproductive apparatus is elevated on a *stipes* (as in the Mushroom tribe), the nutriment, which is entirely received by the mycelium at its base, is transmitted by its elongated cells, and probably through certain hollows left by the separation of the tissue (termed *inter-cellular spaces*), to the expansion on its summit, where it is diffused in every direction.—It may be regarded, therefore, as a general expression of the function in these Cellular plants, that, when there is no tendency to prolongation in a particular direction, and the cells retain their rounded form, they transmit fluid with equal readiness towards all sides; but that, when any separation of the different parts takes place, by the restriction of the function of Absorption to one portion of the surface, there is a tendency to the evolution of an axis formed of prolonged cells, in the direction of which the fluid is conveyed most readily to the other parts of the system; its course being most rapid in those parts in which the laxity of the tissue and the direction of the cells oppose the smallest amount of resistance, just as we see liquids penetrating easily through unsized paper.

199. In the higher group of *Cryptogamia*, consisting of the *Mosses* and *Ferns* with their allies, we find a much more evident approach to the vascular structure and general circulation of the Phanerogamia. Still, however, its lower tribes (such as the *Hepaticæ*, § 27) are so closely

connected with the more perfect forms of the preceding group, that what has been said of those will be equally applicable to them.—Among the *Mosses,* strictly so called, we find several species in which a complete stem is developed, furnished with radical fibres at its base, and bearing a number of veined leaves regularly arranged upon it. In these, the cellular tissue between the central and cortical portions of the stem and in the mid-veins of the leaves becomes considerably elongated, so as almost to resemble woody and vascular structure; it does not appear, however, that fluids are so readily transmitted along this tissue (probably on account of its greater compactness) as they are through the softer parenchyma which envelopes it. It can scarcely be doubted that there is in Mosses a regular transmission of fluid absorbed by the roots, towards the leaves; especially as we find many of them furnished with that special *exhalant* apparatus for the transpiration of fluid, which is fully developed in the more perfect plants (CHAP. VII.)—In the *Ferns,* the evolution of a true woody stem proceeds to a much greater extent; and in this is found a vascular structure, scarcely differing from that of the Phanerogamia. Although little has been observed as to the circulation of sap in this group, it can scarcely be doubted that the fluid absorbed by the roots ascends to the leaves, as in Flowering-plants; and it appears that, as in the least actively-vegetating states of the latter, the sap ascends rather through the cellular parenchyma, than through the 'scalariform vessels,' which generally, if not always, contain air.

FIG. 109.



Longitudinal section of Stem of *Italian Reed:* —*a,* cells of the pith; *b,* fibro-vascular bundle, containing, 1. annular duct; 2. spiral duct; 3. dotted duct with woody fibre; *c,* cells of the integument.

200. We shall therefore pass-on at once to describe the circulation in the *Phanerogamia,* in which it has been more fully investigated; and we have first to speak of the *ascending* current, which is produced by the movement of the fluid that is absorbed at one extremity of the axis, towards the leaves by which a large proportion of it is exhaled at the other.—Each annual layer that composes the wood of the stem of *Exogens,* consists of woody fibre and ducts, intermixed with more or less of cellular tissue (Fig. 109); the vessels being usually situated at the inner part of the ring, and the fibrous tissue, which is not formed until later in the year, lying externally to them. The vessels have usually the greatest diameter in long slender stems, belonging to plants of active vegetation, in which the sap has to be conveyed with rapidity to a con-

siderable distance, as in the Vine and the Clematis; and they are usually larger, also, where the stem is dense, as in the Oak, Elm, Mahogany, &c., than where its softness and laxity allow the whole texture to convey fluid more readily, as in the Pine tribe, which is destitute of any distinct sap-vessels, or in herbaceous plants, in which they are usually small in proportion, or in the young shoots of woody branches in which the intercellular passages abound. In the latter it is probable that the cellular parenchyma always affords the principal channel for the ascent of the sap; and even where the vessels are large, it appears from recent experiments to be only when the sap is ascending rapidly, that they take part in its conveyance, their tubes being occupied at other times by air alone, which is then displaced.* The deposition of the products of secretion, which gives strength and firmness to the *duramen*, destroys or greatly diminishes its power of transmitting fluid; and it is consequently through the external layers, which constitute the *alburnum* or sap-wood, that the movement of fluid chiefly takes place.—Of the precise course of the ascending sap in *Endogens*, we have no certain knowledge; there can be little doubt, however, that it is conveyed through all the tissues of the stem which are not consolidated by interstitial deposit, but more especially by the ducts when these are peculiarly large and open, as is especially the case in long, firm, slender stems, whose leaves are borne at a considerable distance from the roots. Of this arrangement, the various species of *Calamus* or 'reed-palm' (one of which furnishes the well-known 'rattan-cane') present most characteristic examples; the ducts being of great size and freely pervious through considerable lengths, whilst the remaining tissues of their wiry stems are so dense as to be quite unfit for the conveyance of fluid.†

201. The cause of the *ascent* of the sap in the stem has long been a disputed question amongst physiologists; some attributing it altogether

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* See Hoffman 'On the Circulation of the Sap in Plants,' in "Botanische Zeitung," vols. vi. viii., translated by Mr. Henfrey in "Scientific Memoirs," 1853.

† It has been affirmed by Prof. Schleiden, that the idea of the ascent of the sap through vessels is altogether a fiction, created by the imagination of those who have desired to find in Plants the analogues of the Animal functions. But the Author cannot help believing that the desire of that distinguished Botanist to establish the entire *absence* of analogy between the two kingdoms, has much to do with his somewhat dogmatic denial of a movement of fluid through vessels in Plants. And whilst the Author is far from denying that the cells, woody fibres, and intercellular passages of the stem, *all* assist in the transmission of fluid from the roots towards the leaves, he cannot but think that the ducts, when fully developed, are the *special* channels by which this transmission is effected. How else could the ascending sap find its way through the wiry stems of the *Calamus rudentum*, or 'cable-palm,' which are sometimes 500 feet long?—The experiments of Honninger ('Botanische Zeitung,' 1843) upon the absorption of ferro-cyanide of potassium, the course of which upwards through the stem was afterwards tested with sulphate of iron, led him to the conclusion (which has been adopted by Link and other distinguished Botanists) that it is *only* through the tubular tissues of Vascular plants, that fluid ascends. His experiments, however, were chiefly made upon species in which, for the reasons stated in the text, the vessels afford a much readier channel for the sap, than do the other tissues. On the other hand, Mr. Rainey concluded from experiments of a very similar kind, made with bichloride of mercury, that the ascent of sap chiefly takes place in the intercellular passages ("Experimental Inquiry into the Cause of the Ascent and Descent of the Sap," 1847).—The Author cannot but believe that the discrepancies of these and numerous other observations are partly due to differences in the structure of the stems of the respective species upon which they have been made, and partly (as the results of Dr. Hoffman's experiments indicate) to differences in the epoch or activity of vegetation.

to mechanical influences, and some regarding it as a purely vital (and therefore completely inexplicable) phenomenon. A very simple experiment will show that two sets of causes must be in constant operation. If the top of a young tree be cut-off in the spring, and the divided extremity be immersed in water, it will absorb a sufficient quantity of fluid for the temporary supply of the leaves; whilst, on the other hand, the portion of the stem left in the ground will continue for a time to discharge the fluid drawn-up by the roots. It is then evident, that the propulsive power of the roots, for which we have already endeavoured to account (§ 177), is a partial, but not the entire, cause of the ascent of the sap in the stem; since the latter will continue by simple imbibition, when the open extremities of the vessels are placed in fluid, provided that the functions of the leaves are sufficiently active to occasion a demand for it. Moreover, there would seem no reason why the spongioles should not be as capable of absorbing fluid in the winter as in summer; and if the ascent of the sap depended entirely upon them, we should expect that it would be continued. That they are thus capable has been frequently shown, by grafting a shoot of an evergreen upon a stock whose leaves are deciduous; it being found that the uninterrupted continuance of the demand meets with a corresponding supply. A still more striking experiment is to train a shoot of an out-door vine, or other plant, into a hot-house during the winter; the unusual warmth will cause an immediate development of the buds, for which a supply of nutriment is required; and this is derived from the roots, whose usual torpidity at this season is thus remarkably interrupted. Careful examination of the first movement of the sap in spring, also leads to the same result; for it is now ascertained that the upward flow begins near the buds, and that it may be progressively observed in the branches, trunk, and roots,—the latter not commencing their action, until the superincumbent column has been removed. It can scarcely, then, admit of a doubt, that the demand for fluid, occasioned by the vital processes which take place in the leaves, is the essential cause of the motion of the sap in the higher parts of the tree; and that the propulsive power of the roots is principally expended in raising it to the sphere of that influence. It is evident that the quantity of fluid absorbed by the roots, will be proportioned to the rapidity of its removal by the leaves above; just as the continued rise of oil in the wick, by simple capillary attraction, is regulated by the rate of combustion at its apex.

202. It has been commonly supposed that the 'crude sap' of the ascending current is entirely unfit to nourish the growing tissues; and that they derive the materials of their support from a *descending* current of 'elaborated sap,' which is prepared in the leaves, and is thence returned by a distinct set of vessels to the axis, through which it is transmitted even as far as the extremities of the roots. This doctrine, however, can by no means be admitted in the form here stated; although it probably contains a certain amount of truth. The ascending current does not contain those elements *only* which are absorbed from the soil, namely, water, carbonic acid, ammonia, and some mineral ingredients; for, as Prof. Schleiden remarks,* "from whatever part and at whatever time we

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* "Principles of Scientific Botany," translated by Dr. Lankester, p. 505.—The whole of the Section entitled 'General phenomena in the Life of the entire Plant' is worthy of careful study by those who are capable of supplying by their own knowledge what is left unsaid by its learned Author.

examine the sap of a plant, we find that it contains organic principles which cannot come from the soil, because they do not exist there; such are sugar, gum, albumen, malic, citric, and tartaric acids, &c." The presence of these substances in the ascending current is accounted-for by some Physiologists, on the idea that they were previously contained in the tissues, and have been taken-up by it in its progress through them; whilst by Schleiden and others it is affirmed, that they must have been generated by the assimilating action of these tissues upon the materials drawn-in by the roots.* Whichever of these two views is the correct one (and it is possible that both may be partly true), it is certain that the ascending current of sap must be capable of affording nutriment to the growing tissues, in so far as it holds gum, sugar, and albumen in solution; and hence there is no sufficient reason for looking to a supply of 'elaborated sap,' afforded by a hypothetical descending current, as their sole pabulum. But, on the other hand, there appears sufficient evidence that the leaves are the chief agents in the introduction of carbon into the system, by the decomposition of the carbonic acid of the atmosphere (§ 268); and that a much greater quantity of the organic compounds, at the expense of which the new tissues of the plant are formed, is prepared by *their* instrumentality, than by any other means. These organic compounds must be dispersed through the axis; and there appears strong reason to believe that this dispersion is chiefly effected by the *cellular* portion of it, and especially, in Exogens, by the bark (with which the leaf-stalks are in very intimate connection) and by the medullary rays. By the bark, these compounds are especially conveyed to the interspace between the liber and the alburnum, in which the formation of new wood takes place; whilst by the medullary rays they are carried-in towards the centre of the stem, and afford the means of consolidation to the duramen. It is in accordance with this view, that if a ring of bark be removed from a stem, the parts above the ring undergo an unusual amount of increase, whilst those below the ring are comparatively atrophied. There is no reason to suppose, however, that this dispersion is effected by anything like a *current;* still less, that any special system of vessels is provided for conveying back the 'elaborated sap' from the leaves to the stem. Its transmission appears to be simply a process of imbibition, taking place between contiguous cells, whereby each communicates to the rest a portion of the nutritive materials with which it is charged; every one making that use of them which is in accordance with its own endowments.—Additional evidence in favour of the view here advocated, will be given hereafter (CHAP. VIII.)

203. It appears from microscopic observation, however, that a special circulation of peculiar juices does take place in certain parts of particular tribes of plants, through that system of anastomosing vessels, which has been termed *laticiferous* (Fig. 110). This *cyclosis* has been only observed in plants with 'milky' juices, that is, in those which have a 'latex' rendered opaque by the presence of floating particles of resin, caoutchouc, or other substances; and it is altogether questionable, whether this 'latex'

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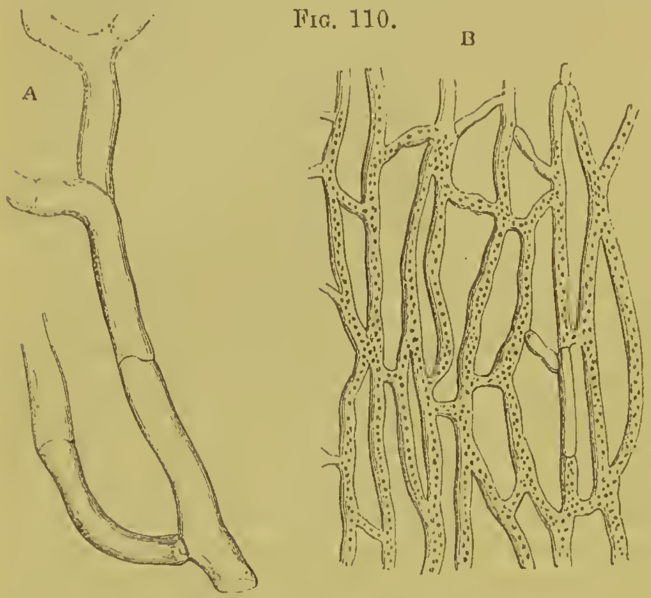
* It is difficult to understand, however, how this process can be effected by the cells of the interior of the stem and roots, secluded as they are from the direct influence of light; without which (we have every reason to believe) no direct production of organic compounds from inorganic elements can take place.

is not peculiar to the plants with milky juices, and is not rather to be considered in the light of a special secretion, than as a nutritious fluid. When the laticiferous vessels are cut or broken across, a flow of fluid takes place from the wounded part; and if a piece of the bark or leaf of a 'milky' plant be cut out and placed under the microscope, the fluid contained in the vessels will be seen in rapid movement throughout. This, however, has no relation to the true circulation, which was first described by Prof. Schultz as taking place in the laticiferous vessels of an uninjured part.* The movement seems to take place in all directions, the currents often running contrariwise in contiguous vessels. Sometimes one of these currents may be observed to stop, its cessation being preceded by a temporary oscillation; it afterwards recommences, or a new current is established in a contrary direction. The rate

Fig. 110.



Laticiferous vessels:—A, their formation from cells; B, network of milk-vessels from the stipule of *Ficus elastica*.

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* "Nova Acta Acad. Nat. Curios.," vol. xviii., and "Ann. des Sci. Nat.," 2^e Sér. Botanique, tom. vii.—The statements of Schultz have been called in question by many distinguished Botanists, amongst others by Prof. Schleiden, who have regarded the movements described by him as the result of injury to the vessels, permitting the discharge of their contents, and consequently establishing a current towards the point of exit. So many competent observers, however, have satisfied themselves that such is not a sufficient explanation, that the existence of a regular movement of the latex in *certain plants* must, in the Author's opinion, be regarded as an established fact, whatever be its degree of generality. The latest recorded observations on this point are those of Prof. Balfour; which are to the following effect.—"From observations made last summer, I am disposed to agree with Schultz's statements. It is true, as Mohl remarks, that any injury done to the part examined, causes peculiar oscillatory movements, which speedily cease. Thus if the young expanded sepal of the *Celandine* is removed from the plant and put under the microscope, or if the inner lining of the young stipule of *Ficus elastica* be treated in a similar manner, very obvious motion is seen in the granular contents of the vessels, and this motion is affected by pricking the vessels or by pressure. In order to avoid fallacy, however, I applied the microscope to the stipules of *Ficus elastica* while still attached to the plant, and uninjured; and I remarked that, while pressure with any blunt object on the stipule caused a marked oscillation in the vessels, showing their continuity, there could, nevertheless, be observed a regular movement from the apex towards the base, independent of external influences, when the stipule was simply allowed to lie on the field of the microscope, without any pressure or injury whatever. This movement continued for at least twenty minutes during one of the experiments, and I have no doubt might have been observed longer. It is of importance to distinguish between those molecular movements which are caused by injury and pressure, and those which depend on processes going on in the interior of the living plant. My experiments are by no means complete; but they lead at present to the adoption of Schultz's opinion relative to the existence of the cyclosis."—"Manual of Botany," 1849.

of movement is greatest in parts which are in progress of development, other things remaining the same; it is also accelerated, within certain limits, by warmth; and is retarded or entirely brought to a stop by cold, recommencing on the renewed application of warmth. A strong electric shock puts an end to it immediately.

204. The resemblance between this movement in Plants and the capillary circulation in Animals, makes it a point of peculiar interest and importance to determine the nature and source of the forces by which the former is sustained. It is quite obvious that the movement cannot be due to any *vis à tergo;* both because it is far from being constant in its direction in particular vessels, and because there is no organ to supply a propelling force, which could extend itself through such a complex system of anastomosing canals. Nor, again, can we attribute it to any *vis à fronte*, like that which takes part in producing the ascending current from the roots towards the leaves. It is certain, too, that no such contraction of the laticiferous vessels themselves takes place, as could be effectual in propelling the fluid through them. Further, the movement continues for some time in parts that have been completely detached from the rest, and on which neither *vis à tergo* nor *vis à fronte* can have any influence. On the other hand, the facts stated in the preceding paragraph all indicate that, like the 'rotation' within the individual cells of Plants (CHAP. VIII.), the movement of fluid within the laticiferous vessels (whatever may be its purpose in the vegetable economy) is intimately connected with the formative operations of the part, and is dependent upon forces which arise out of these. The manner in which they become so, is the next object of our enquiry; and on this subject, some views have been put forth by Prof. Draper,* which seem to help towards an explanation of the phenomena.

205. It is capable of being shown, by experiments on inorganic bodies, that, if two liquids communicate with each other through a capillary tube, for the walls of which they both have an affinity, this affinity being stronger in the one liquid than in the other, a movement will ensue; the liquid which has the greatest affinity being absorbed most energetically into the tube, and driving the other before it. The same result occurs when the fluid is drawn, not into a single tube, but into a network of tubes permeating a solid structure; for if this porous structure be previously saturated with the fluid for which it has the less degree of attraction, this will be driven out and replaced by that for which it has the greater affinity, when it is permitted to absorb this. Now if, in its passage through the porous solid, the liquid undergo such a change that its affinity be diminished, it is obvious that, according to the principle just explained, it must be driven out by a fresh supply of the original liquid, and that thus a continual movement in the same direction would be produced.—Now this is precisely what seems to take place in an organised tissue that is permeated by a fluid, between whose particles, and those of the tissue which it penetrates, affinities exist, which are concerned in the formative changes that take place during its circulation. For these affinities are continually being newly developed by acts of growth, as fast

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* "On the Forces which produce the Organisation of Plants," by John William Draper, M.D., New York, 1844; pp. 29 *et seq.*

as those which previously existed are satisfied or neutralised by the changes that have already occurred; and thus in the circulation of the nutritive fluid, there is a constant attraction of its particles towards the walls of the vessels, and a continual series of changes produced in the fluid as the result of that attraction. The fluid, which has given up to a certain tissue some of its materials, no longer has the same attraction for that tissue; and it is consequently driven from it by the superior attraction then possessed by the tissue for another portion of the fluid, which is ready to undergo the same changes, to be in its turn rejected for a fresh supply. Thus in a growing part, there must be a constantly-renewed attraction for that portion of the nutritive fluid which has not yet traversed it; whilst, on the other hand, there is a diminished attraction for that which has yielded-up the nutritive materials required by the particular tissues of the part; and thus the former is continually driving the latter before it. But the fluid which is thus repelled from one part, may still be attracted towards another, because that portion of its contents, which the latter requires, may not yet have been removed from it; and in this manner the current may be maintained through the whole capillary network, until the liquid has been entirely taken up by the tissues which it permeates. The source of the movement being thus attributable to the formative actions to which it is subservient, it is obvious that it must be affected by any external agencies which quicken or retard these; and it is thus that the influence of heat, cold, and electricity upon the rate of the flow seem most readily explicable.—These principles will be hereafter shown to have a most definite application to the phenomena of the 'capillary circulation' in Animals (§ 251).

206. The *development* of the Circulating system during the growth of Vascular Plants, has not yet been made an object of special attention; the general facts with which we are acquainted, however, correspond exactly with the principles which have been previously stated.—As the absorption of nutriment by the embryo within the ovule appears to take place through the whole surface, there is no transmission of fluid from one portion to another; nor do we find, even at the period of the ripening of the seed, any distinct vascular structure. As far as its circulating system is concerned, therefore, the young plant, at the commencement of germination, is on a level with the simpler cellular tribes. During the rapid longitudinal development, however, which then takes place in the stem and root, there is of course a peculiar transmission of fluids in those directions; and this appears to be at first performed, as in the stem of the Fungi, by elongated cells and intercellular passages. It is not until the true leaves are expanded, that we find true ducts in the stem, formed by the coalescence of linear series of cells,* mostly containing spiral fibres or some other secondary growth in their interior; and it is very interesting to remark, that these ducts in young plants often present the appearance which is characteristic of the Ferns, having the spiral fibre more or less regularly disposed within them (Fig. 109, 1, 2); whilst, after the stem has ceased to increase rapidly in length, these canals are converted into dotted ducts (Figs. 109, 3). The anastomosing vessels of the latex in like manner

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* This view of the mode in which the ducts of Plants are formed, based on a comparison of the various forms which they present, has been confirmed by the recent observations of Dr. Hobson on the history of their development. ("Ann. of Nat. Hist.," vol. xi. p. 72.)

originate from cells of less regular form, which open into one another at several points, and not, as in the formation of ducts, by their extremities alone. This change is represented in progress in Fig. 110, A.

3. *Circulation in Animals.*

207. In following the evolution of the Circulating system through the Animal scale, it will be easy to discover its conformity to the same general plan, as that which has just been traced-out in the Vegetable kingdom. In proportion as the power of absorbing aliment is restricted to one part of the surface, whether external or internal, does it become necessary that means should be provided for conveying the nutritive fluid to distant organs; not merely that it may furnish the supplies which they are constantly requiring for the maintenance of their respective structures, and for the manifestation of their vital properties; but also that it may itself undergo certain changes, which are essential to the continuance of its characteristic qualities. Not only does the Circulation of fluid through the system enable the new materials to be deposited in their appropriate situations, but it also takes-up and removes the particles, which, having manifested a tendency to decomposition, are no longer fit for the offices which they previously contributed to perform; so that, by the various processes of elimination, these may be separated from the general mass, and be either appropriated to some other purpose in the economy, or be altogether carried out of the structure. The excretion of carbonic acid by the Respiratory apparatus is one of the most considerable and important of these processes; and it will be found that the distribution of the Circulating system has always an express relation to the conditions under which this is performed. In fact, so peculiar is this adaptation in the higher Animals, that many have considered the sanguiferous system under two heads,—that belonging to the *general* circulation of nutritious fluid through the body,—and that which performs the *respiratory* circulation, conveying the blood, which has been rendered impure by the changes it has previously undergone, to the organs where its physical and vital properties are to be renewed by contact with the air. Respiration differs not in *kind*, however, from the other functions of purification, but only in its relative importance; and although in warm-blooded Vertebrata, whose nervo-muscular energy can only be maintained in full vigour by a constant supply of oxygenated blood, its cessation even for a short time is fatal, there are many amongst the lower classes, in which it can be suspended for a considerable period with impunity, and in which the increased amount of other secretions appears to counterbalance the diminution in its products. We find too, even in the highest Vertebrata, peculiar modifications of the circulating apparatus in connection with other secreting organs, as the Liver in Mammalia, and the Kidneys in Birds; and yet more remarkable modifications of the same nature are elsewhere found: so that it should rather be stated as a general fact, that, in proportion to the variety of the organs, and the importance of the functions they perform, is the special adaptation of the Circulating apparatus which supplies them,—than that it undergoes modification according to the conditions of the respiratory system alone, as Cuvier maintained. In proportion as the function of Absorption is restricted to one part of

the surface, that of Respiration will be limited to another; and the processes of Nutrition, and the formation of Secretions, will go-on in parts of the structure distant from both; and all these must be brought into harmony by the Circulating system, the arrangement of which will evidently vary from the most simple to the most complicated form, according to the number and variety of the actions to which it is subservient, and the vigour with which these are performed.

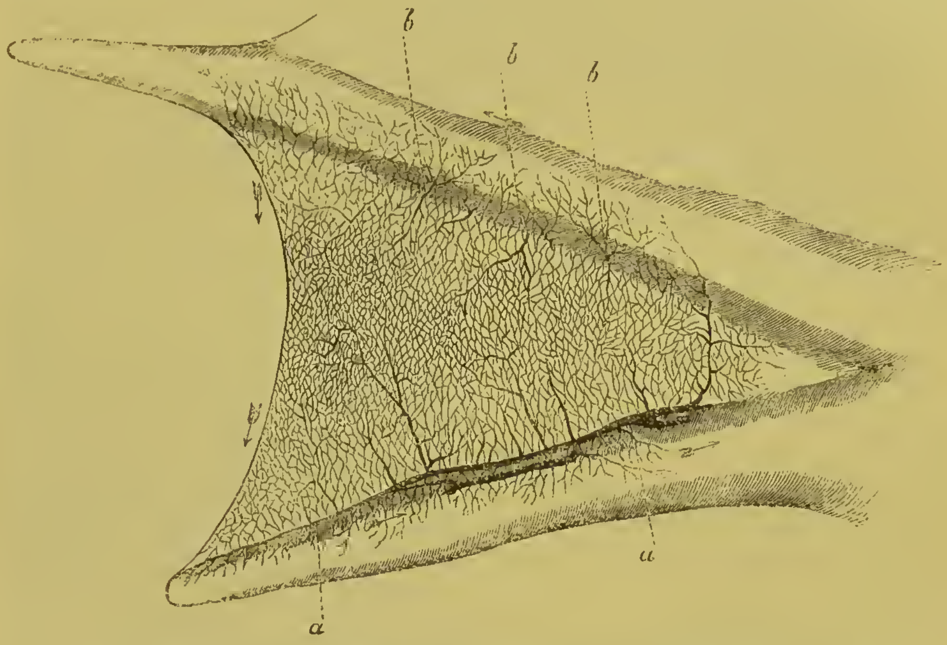
208. Still, in most of those animals whose Nervo-Muscular energy is the greatest, the arrangement of the Circulating apparatus, and the rate of the movement of blood through it, appear to have special reference to the demand for oxygen created in the discharge of the Animal functions, and to the necessity for the removal of the carbonic acid generated in the same processes; whilst there is evidence that the organic operations of growth and development might be carried-on by means of a much less rapid flow, and by a less perfectly-oxygenated blood. A remarkable example of this principle is presented by the condition of the Circulation in the class of Insects, in which the activity of the animal functions is relatively greater than in any other group; for we find that the movement of their nutritive fluid, which is subservient in them to nutrition alone, is comparatively slow and feeble (§ 224), the very active aeration of their nervo-muscular apparatus being accomplished, not so much by the medium of their blood, as by the penetration of air-tubes into the tissues themselves (§ 302).

209. The Circulating apparatus of Animals, at least where it is distinctly developed, differs in one important particular from that of Plants. We have seen that, in the latter, the sap which has been elaborated in the leaves is dispersed through the fabric, giving-up its nutritive constituents to the parts to which it finds its way (§ 202); and if any of it mixes with the ascending current, and circulates a second time through the system, the amount of this is comparatively small. In the higher Animals, on the contrary, we observe that the same fluid is repeatedly transmitted through the body; the alterations which are effected in one part of its course by the withdrawal of materials for particular processes of Nutrition, being counterbalanced in others by nutritive operations of some different kind (see CHAP. VIII.), as likewise by those of Respiration and Secretion, and by the continual admixture of new alimentary materials.

210. In all the higher forms of the Circulating apparatus, again, we find a central organ of impulsion, the *Heart,* into which the fluid returned from the various parts of the body is poured, and on whose contractile force the maintenance of the current chiefly depends. From this it passes-out by one or more large trunks, which convey it to the several organs and tissues; these are called *Arteries.* The arteries gradually subdivide into ramifying vessels, which, repeatedly undergoing the same change (Fig. 111), terminate in a complex system of *anastomosing* (intercommunicating) tubes, of nearly uniform size, which are termed *Capillaries.* It is in these only, that the blood comes into sufficiently intimate relation with the tissues which it supports, or by which secretions are elaborated from it, for the performance of chemical or vital reactions between them; so that we may consider the function of the arteries to be the simple conveyance of the nutritive fluid from the central organ of

impulsion to this network of capillaries, which exists in most of the living tissues of the body, and in near proximity to the remainder. Even the walls of these trunks are furnished with a distinct set of branches (the *vasa vasorum*), proceeding from neighbouring vessels, for their own nutrition. After traversing the capillaries, the blood is received into another series of vessels, formed by their reunion, which are termed *Veins;* and these, gradually coalescing into larger trunks, return it to the central reservoir.—The walls of the Arteries and Veins are formed of several layers of tissue, which, however, constitute three principal 'coats.' The *inner* coat is a pellucid structureless membrane, continuous both with that which lines the heart, and with that which forms the sole boundary of the capillaries; and this is covered on its free or internal surface by a layer of epithelial cells. The *outer* coat is simply protective, and is formed of condensed areolar tissue. The *middle* or 'fibrous' coat, however, which is much thicker in the arteries than in the veins, is partly composed of yellow elastic tissue; and partly of non-striated muscular fibre. By the agency of the former, which is especially abundant in the larger arteries that receive the blood direct from the heart, the intermitting jets in which the fluid is at first propelled by its contractions, are gradually converted into a continuous stream. The latter, on the other hand, is more abundant in the smaller arteries, and appears to supply a propulsive force in some degree complementary to that of the heart; but its main purpose seems to be, to regulate the diameter of the vessels, in doing which it is probably influenced in some degree by the Sympathetic system of nerves that is minutely distributed upon it. Of rapid alterations in their diameter, which, being emotional in their source,

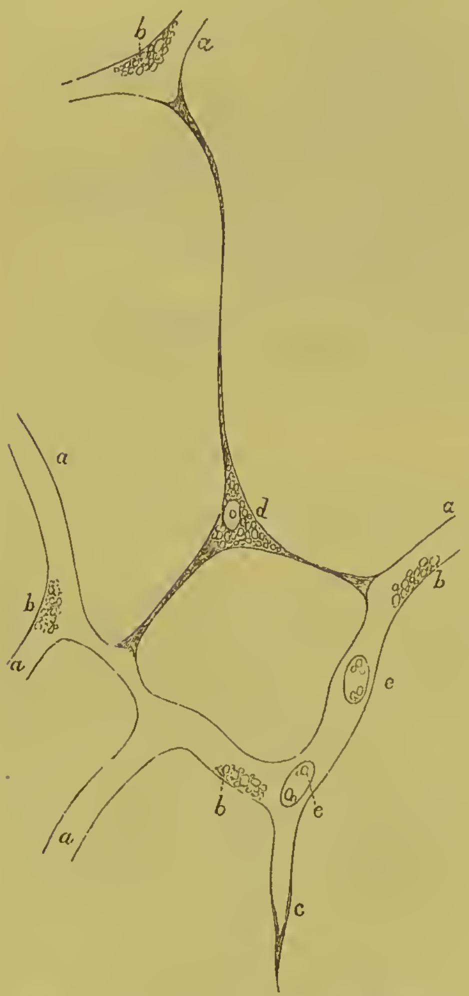
FIG. 111.



Web of *Frog's* foot, stretching between two toes, magnified 3 diameters; showing the blood-vessels, and their anastomoses: *a, a,* veins; *b, b, b,* arteries.

can be only referred to the instrumentality of the nervous system, we have a characteristic example in the act of 'blushing.'—The capillary vessels, too, in the higher animals, possess a distinct wall, which is continuous with the lining membrane of the larger vessels; and they are thus to be considered in a different light from that of a mere system of passages excavated in the substance of the tissues.

Fig. 112.



Formation of *Capillaries* in tail of Tadpole:—*a, a,* capillaries permeable to blood; *b, b,* fat granules attached to the walls of the vessels, and concealing the nuclei; *c,* hollow prolongation of a capillary ending in a point; *d,* a branching cell, with nucleus and fat granules, communicating by three branches with capillaries already formed; *e,* blood-corpuscles, still containing granules of fat.

211. The trunks and branches of the Blood-vessels appear to be formed, in the first instance, like the ducts of Plants (§ 206), by the coalescence of cells arranged in linear series; those of moderate size taking their origin in single or double files of such cells, whose coalesced walls form the primitive simple membranous tubes of these vessels; whilst the principal trunks, like the heart (§ 248), are formed out of aggregations of cells, of which those in the interior liquefy to form the cavity, whilst those on the periphery are metamorphosed into the fibrous and other tissues of which their more substantial walls are composed. The first Capillary network, however, seems to be formed by the coalescence of prolongations of stellate cells (Fig. 112), which come into contact either with the walls of vessels already existing, or with each other; and when their cavities have become continuous with those of vessels previously traversed by blood, they too begin to receive that fluid, then enlarge, and at last form a regular network of tubes,—their cellular origin, however, being still indicated by the presence of nuclei in their walls.* The subsequent development of capillaries, on the other hand, usually takes place by outgrowth from the vessels previously formed; in the mode thus described by Mr. Paget.† "Suppose a line or arch of capillary vessel, passing below the edge or surface of a part to which new material has been superadded. The vessel will at first present a slight dilatation in one,

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* See the observations of Prof. Kölliker 'Sur le développement des Tissus chez les Batraciens,' in "Ann. des Sci. Nat.," 3^e Sér., Zool., Tom. vi.

† "Lectures on Surgical Pathology," vol. i., p. 216.

and coincidently, or shortly after, in another point, as if its wall yielded a little, near the edge or surface. The slight pouches thus formed gradually extend, as blind canals or diverticula, from the original vessels, still directing their course towards the edge or surface of the new material, and crowded with blood-corpuscles, which are pushed into them from the main stream. Still extending, they converge, then meet; the partition-wall that is at first formed by the meeting of their closed ends, clears away; and a perfect arched tube is formed, through which the blood, diverging from the main or former stream, and then rejoining it, may be continuously propelled."—This last process may be seen in the growing parts of the tail of the Tadpole, in the development of the filamentous gills and of the legs of the Water-Newt, in the first evolution of the extremities of the embryoes of higher animals, and in the formation of new structures in the fully-developed organism, either for the repair of injuries, or as the result of morbid processes. In some instances it would appear that the wall of the newly-forming vessel gives way, and that the blood-corpuscles escape from it into the parenchyma, at first collecting in an undefined mass, but soon manifesting a definite direction, and coming into connection with another portion of the arch or with some adjacent vessel. Thus, then, a *channel* and not a *vessel* is formed; and it is probably in this way that those passages are excavated, which take the place of distinct vessels in many of the lower tribes of animals.

212. The foregoing description, however, is by no means applicable to the entire Animal kingdom; for in many of the simpler tribes, there is no circulation of a proper nutritive fluid; and in many others, the vascular system is far from possessing the completeness of organisation which it exhibits in the higher groups. An entire deficiency of any special provision for this purpose, is seen alike in such among the lower tribes of Animals as possess no digestive cavity, and in such as have the digestive cavity or its prolongations extending through their whole fabric. To the first category belong the *Cestoid* Entozoa (§ 138), which derive the whole of their aliment by imbibition of the juices of the animal they infest, through the soft integument with which their bodies are everywhere covered. Notwithstanding the specialized condition of some parts of their organisation, therefore, they are on the level of the Algæ as regards the general diffusion of the power of absorption; and there is consequently no occasion for any circulation of nutrient fluid through their bodies. In the second category we find the *Trematode* Entozoa,* and the classes of *Zoophytes* and *Acalephæ* among the Radiata; for, as already shown (§§ 151—154), the digestive cavity of these animals is either itself in such immediate relation to their tissues, that they can supply themselves directly by imbibition with the alimentary materials which it has prepared; or it so communicates with the visceral cavity, that these

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* A system of *vessels*, which have been until lately reputed to be sanguiferous, does indeed exist in both the above named tribes of Entozoa: but it seems now quite certain that these vessels, together with the trunks which in the Cestoidea have been regarded as constituting an alimentary canal, really belong to the 'water-vascular' system of Siebold. What is the nature of their contents, and what is the purpose of the movement which is seen in them, are still far from being clearly known. But as, on the whole, this system of vessels appears most to resemble the 'respiratory tree' of the Holothurida (§ 284), it will be described in connection with the Respiratory organs generally (§ 285).

materials find their way through the latter to the parts not in immediate contact with it; or, again, a system of lacunæ or of channels is prolonged, either from the digestive or from the visceral sac, into parts which are far removed from the principal cavity of either.

213. The simplest provision for a proper Circulation of nutritive fluid, consists in the complete separation of the Digestive cavity from the 'general cavity of the body;' the immediate products of the digestive operation being limited to the former; whilst the latter is filled with a 'chylaqueous fluid' (§ 40, *note*), the materials of which have transuded into it through the walls of the alimentary sac or tube which it surrounds. This fluid resembles the chyle of Vertebrata, rather than their blood, in the low proportion of its organic to its aqueous components, in its imperfect coagulating power, in the absence of colouring matter, and in the nature of the floating corpuscles which it contains. In the simpler forms both of Articulated and of Molluscous animals, we find the flux and reflux of this chylaqueous fluid in the general cavity of the body,—maintained by no special provision, but due only to movements that are related immediately to some other purpose,—constituting the only provision for supplying the organs generally with nutriment, and for keeping the nutritious fluid itself in the requisite state of aeration. This is the case, for example, with the *Rotifera* and *Bryozoa*, which, in this respect, are upon the same grade of development; it is the case, too, with the small tribe of *Pycnogonidæ* (§ 231), even in their permanent condition; and it seems to be true also of the larval condition of certain Myriapods and Insects. The group of *Nematoid* Entozoa, too, in which the intestinal canal lies freely in the midst of the visceral cavity (Fig. 52), seems to rank in the same category, together with a group of inferior worm-like animals of similar organisation, which inhabit fresh waters and seas; for although they have a system of vessels which has been regarded as sanguiferous, it is almost certain that these vessels belong to the same category with those of the other Entozoa, and that whatever circulation of nutritive fluid may take place in their bodies, it is restricted to the visceral cavity, with which the tissues generally are in immediate contact.

214. As we ascend from the lower Mollusca and Articulata towards the higher members of each sub-kingdom, we find that the Circulating system is gradually developed as an offset (so to speak) from the visceral cavity. This is seen most clearly in the Tunicated Mollusks, which, whilst very closely allied to the Bryozoa, are superior to them in this particular; for the whole sinus-system through which the blood is carried, not merely to the body generally, but also to the respiratory organs, is but a prolongation of this cavity, with which it remains in the freest communication; and the heart is but a portion of one of these sinuses, partially or completely surrounded by a muscular envelope. This state has its parallel among the Articulata, in the condition of the circulating system of many Insect-larvæ, as also in that of many Entomostracous Crustaceans, and perhaps in some of the lower forms of Arachnida. Proceeding higher, however, we find the heart becoming more and more muscular, and the arteries that proceed from it acquiring distinct parietes; the blood which has been distributed by these, however, becomes dispersed through the lacunæ between the tissues and organs; and before returning

to the heart, it passes into the visceral cavity, which may itself be so contracted, as to present the semblance of a large venous sinus. Throughout the Invertebrated series, with two exceptions which are perhaps rather apparent than real, we may trace this connection of the Circulating system with the 'general cavity of the body;' and it is only among the Vertebrata (with these exceptions) that we find the sanguiferous system forming a completely *closed* current. The only trace that seems to remain in that series, of the *lacunar* circulation so universal in the inferior classes, is at the commencement of the Lymphatic system of Absorbents; which seem to take up, for return into the circulating current, the surplus of such nutritious fluid as may have escaped from the capillaries into the interstices of the tissues (§ 192).[*]

215. The only class among the Radiata in which a proper Circulation of nutrient fluid takes place, is that of *Echinodermata;* but the true nature of this circulation is far from being entirely understood. It seems unquestionable, from the recent investigations of M. de Quatrefages (op. cit.) and Dr. T. Williams (op. cit.), that a very important, if not the principal part, in the distribution of the nutritive materials that have transuded through the walls of the digestive cavity, is here performed by the movement of the 'chylaqueous fluid,' which is the product of that transudation, through the 'general cavity of the body;' this movement being kept-up by the vibration of the cilia which clothe its lining membrane. And it is further remarkable that the principal provisions for aeration which we meet-with in this class, are applied to the 'chylaqueous fluid' of the general cavity, rather than to the fluid (blood?) contained within the more special vascular system (§ 284).—The existence of a system of vessels apparently sanguiferous, in some of the principal types of the group, has long been known; but many points relating to its minute distribution, as well as in regard to its functions, yet remain to be elucidated. In particular, it is a point of great interest to determine whether or not it communicates in any part of its course with the 'general cavity of the body,' as the analogy of Invertebrated animals generally would lead us to expect, if its function be really the circulation of *nutritive* fluid; for it can hardly be thought probable, that even in the most elevated forms of the Radiated sub-kingdom, the special circulating apparatus (which is not found to exist in any group of animals below them) should at once attain a character of the highest elevation, in such a complete 'closure' as is not presented even by the most elevated Mollusca or Articulata. The recent observations of Müller and Leydig appear to show that such communications do exist; and the observations of Dr. T. Williams upon the identity, alike chemical and morphological, between the chylaqueous fluid and the contents of the vascular system, are to the same purpose. If, too, as is also affirmed by Dr. T. Williams, the vascular trunks are lined with cilia, and their contained fluid is propelled by ciliary agency, a very strong case will be undoubtedly made out in favour of the doctrine, that the vascular system which has been supposed to be

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[*] See the admirable Memoir of Prof. Milne-Edwards, 'Observations sur la Circulation,' in "Ann. des Sci. Nat.," 3^e Sér., Zool., Tom. iii.; that of M. de Quatrefages 'Sur la Cavité Générale du Corps des Invertébrés,' Op. cit., Tom. xiv.; and that of Dr. T. Williams 'On the Blood-proper and Chylaqueous Fluid of Invertebrated Animals,' in "Philos. Transact." 1852.

'closed' in this class, is either a diverticulum from the general cavity of the body, as in other Invertebrata, or, like the supposed sanguiferous system of Annelida (§ 219), is a peculiar form of the Water-vascular system.—Both as to the arrangement of this system, and as to its degree of development, a considerable difference seems to exist among the principal sections of the class.

216. In the *Asterias,* in which the digestive cavity is prolonged into the 'rays' or lobes of the body (Fig. 37), a 'mesenteric' trunk is found lying on the surface of each of the radial cæca; and the several trunks, converging from the rays to the central disk, unite with other branches from the stomach, to form a circle or vascular ring around the upper part of the disk. This is connected with a similar ring surrounding the entrance to the stomach on the lower surface, by means of a vertical descending vessel, which Tiedemann found to possess muscular irritability, and regarded as the rudiment of a heart; whilst, from the lower ring, other vessels proceed which are distributed through the disk and rays. No capillary network, however, nor even any system of minute ramifications, has yet been traced in continuity with these trunks.—In the *Echinus,* two vascular trunks are found to run along the intestine, one of which is supposed to be venous, the other arterial. The supposed mesenteric vein passes towards the oral orifice, where it terminates in a vascular ring, with which is connected a contractile vesicle, resembling that of Holothuria (Fig. 40, *p*), but of more prolonged form. From this oral ring are given-off five vessels which supply the parts connected with the mouth, five trunks which pass along the ambulacral regions in the membrane lining the general cavity of the body, and another trunk, apparently arterial, which runs along the border of the intestinal tube. The ambulacral trunks converge again towards a vascular ring that surrounds the anus; whence also are given off trunks for the supply of the ovaries.—In the *Holothuria,* the vascular system attains a far higher degree of development; for the trunks subdivide into ramifications of greater minuteness, and the fluid they contain is therefore more extensively distributed. The same general plan may be traced, as in the preceding cases; but with variations which seem to have reference to the more special development of the respiratory apparatus in this order, as well as to its transitional character. The intestinal system of vessels consists of a long trunk, doubled on itself, which passes along the *external* margin of the intestine (Fig. 40, *v e*), and which ramifies minutely upon its surface; its two inflexions being directly connected by the anastomotic branch *v a, v a'*. The ramifications of this trunk, along the upper part of the intestine, seem to terminate directly in those of the *internal* intestinal vessel *v i;* but those of the middle part of the alimentary canal are continuous with those of the mesenteric trunk *v m;* whilst between this last trunk and the internal intestinal trunk, is a series of minute plexuses *v r.* The course of the blood through this system of vessels has not been positively determined; but it would seem probable that one of the intestinal trunks is venous and the other arterial, and that the minute distribution of the blood-vessels upon the walls of the intestinal canal has reference to the introduction of fresh nutritive materials into the sanguiferous circulation; whilst it can scarcely be doubted that the mesenteric plexus is subservient to respiration, though it does not come

into immediate relation with the 'respiratory trees' (§ 284). Besides this system of vessels, there is another, consisting of an annular trunk (*va*), which surrounds the mouth (as in Echinus), and sends off branches to the buccal apparatus and to the tentacula (*t*), as also to a set of tegumentary vessels (*vl*, *vl'*), which supply the general surface. In connection with the œsophageal collar is found a saccular dilatation (*p*), which seems to represent the pulsatile vessel of the Echinus; but whether it possesses a similar contractile power, is not known. The connection of this set of vessels with the preceding has not yet been made out.

217. The *Articulated* classes are usually regarded as inferior to the Mollusca in the evolution of their circulating apparatus; and it certainly never presents the same concentrated condition in the former group, as in the latter. There are some extensive groups in this sub-kingdom, as already remarked (§ 212), in which there does not appear to be any other circulation than such as may take place in the 'general cavity of the body;' the fluid in its lacunæ being continually put in motion by the movements of the animal, and being thus driven from one part of the body into another. Amongst the lowest Articulated animals which have been until recently supposed to possess a proper blood-vascular system, this can no longer be regarded in its former light; and we shall see that even in the case of the Annelida, a considerable modification of previous views may not improbably be required. Where a Sanguiferous system unquestionably exists, it appears to be constantly formed upon the following plan. A vascular trunk passes along the dorsal region, in which the blood passes from behind forwards, being propelled by the contractions of its walls; this trunk, in its typical development, is divided by transverse valvular partitions into as many chambers as there are segments of the body; and by the successive contractions of the walls of these chambers, the circulating fluid, which enters at the posterior extremity of this 'dorsal vessel,' or which is received into it at any portion of its length, is propelled forwards through a principal trunk which is continuous with its anterior extremity, as well as through smaller vessels proceeding from the chambers to their own segments. This arrangement, however, is seldom completely carried-out. For in the lowest forms of this 'dorsal vessel,' although it is distinctly contractile through its whole length, there is no division into chambers; whilst in the highest, a considerable portion of it is destitute of propulsive power, only a few chambers, or even but a single one, being endowed with muscular contractility. The blood propelled forwards and distributed by the *dorsal* vessel, is collected and returned to the posterior part of the body by a *ventral* trunk.—As in most other parts of the nutritive apparatus of this group, it may be observed that a very exact bi-lateral symmetry prevails, alike in the central organs, and in the peripheral distribution of the blood-vessels.

218. A large share in the distribution of nutritive materials through the system of the Annelida, is undoubtedly taken by the 'general cavity of the body;' which not only surrounds the alimentary canal throughout its whole length, but also sends prolongations into the greater number of the appendages that are given off, as well from the head, as from the trunk. The fluid contained in this cavity is richly corpusculated and coagulable; and it is kept in continual movement by the contractions and extensions of the different segments of the body, which most of these

animals are incessantly performing. The visceral portion of the cavity is sometimes almost completely divided by transverse inflections of its lining membrane, into segmental chambers; but these always communicate with each other more or less freely, so that there is a continuous passage for their contained fluid from one part of the body to another. This fluid, when seen in motion within the cirrhi and other appendages into which it freely passes, has been usually considered as *blood;* but it is obviously to be regarded in the same light as the 'chylaqueous fluid' of inferior animals; yet when its composition, the universality of its diffusion, and the obvious provisions for its aeration, are together taken into account, it seems impossible to resist the inference, that it is scarcely less essentially subservient to the nutrition of the fabric, than is the blood of higher animals. In certain degraded Annelida, indeed, no vascular system exists; and it is obvious that the movement of the chylaqueous fluid through the visceral cavity and its prolongations must there be the sole representative of the circulation.*

219. In by far the greater number of animals belonging to this class, however, there is a vascular system of very remarkable character; consisting of a set of trunks and vessels, usually furnished with a multiplicity of organs of impulsion, and subdividing into ramifications of great minuteness. The extent and mode of distribution of this vascular system differ greatly in the several sections of the class; but they obviously have reference in great degree to the amount of specialization, and to the mode of arrangement, of the Respiratory apparatus. The fluid which they contain is usually coloured, being very commonly red, sometimes green, more rarely of a yellowish or brownish hue, and occasionally colourless; but *it seldom or never contains corpuscles;* and in this respect, therefore, it departs so widely from the usual character of a nutritive fluid, as to suggest a strong doubt whether it be truly blood, and whether the vessels which contain it ought to be regarded as the representatives of the sanguiferous system of higher animals. This doubt derives additional force from the greater degree of resemblance which this vascular system of Annelida bears to the 'aquiferous system' of the Trematoid Entozoa (§ 286), the Nemertine Worms, &c. (the connection between the two being established by the Leech and its allies), than to the typical form of the sanguiferous system of the Articulated sub-kingdom as it exists in Myriapoda; and from the very anomalous character which it would present, if really sanguiferous, in being the only known example in the whole Invertebrated series, of a blood-vascular system not communicating freely with the general cavity of the body. It seems far from improbable, however, that the function of this apparatus is essentially respiratory; and that it may perform the function of the sanguiferous system in distributing a highly aerated fluid through the body for the oxygenation of its tissues, whilst the movement of the chylaqueous fluid through the general cavity answers the purposes of nutrition.†

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* See the Memoirs of M. de Quatrefages and of Dr. Williams already cited; and the 'Etudes sur les Types inferieurs de l'Embranchement des Annelés,' by the former of these observers, in the "Ann. des Sci. Nat.," 3e Sér., Zool., Tom xiv.

† The question above stated with regard to the real nature of the vascular system in the Annelida, was first suggested to the Author by his friend Mr. T. H. Huxley; whose doubts on this point appear to him fully justified by the evidence which will be adduced hereafter, in regard to the 'water-vascular system' of the Entozoa and their allies. There

220. In the *Leech* and its allies, which constitute the division of this class that is most nearly allied to the inferior Annulosa, four principal longitudinal trunks may be distinguished; namely, a dorsal, a ventral, and two lateral. The *lateral* trunks alone seem to be endowed with propulsive power; and they appear to contract and dilate alternately with each other. They send off branches which form a plexus underneath the skin; and this distribution of the circulating fluid seems to have reference chiefly to its aeration, there being no more special provision for that purpose. The lateral trunks communicate freely with each other by transverse arches, into which a continual stream of blood is poured by the contraction of one or other of them; and this is distributed, by vessels proceeding from the arches, to the intestinal canal, the generative organs, and also to a set of looped vessels which proceed to a row of sacculi on each side of the body, that have been variously regarded as respiratory organs, as muciparous follicles, and as representing the 'water-vascular' system,—the latter view being probably the correct one (§ 286). From these various parts it is conveyed to the cutaneous plexus, chiefly through the two median (dorsal and ventral) trunks; and in this plexus it seems to execute an oscillatory movement from one side to the other, by the alternating impulses of the lateral trunks, into one or other of which it will at last find its way, to recommence its movement through the body generally.*

221. In the *typical* Annelida, the most constant parts of this apparatus are the dorsal and ventral trunks; the lateral vessels, however, often exist, although they are seldom of the same relative importance as in the Suctoria; and the dorsal and ventral trunks are themselves sometimes double along a part or the whole of their course, running on the two sides of the median line, or at a little distance from it, like the longitudinal vessels in the Entozoa (Fig. 136). Moreover, we generally find special contractile dilatations on some part of the vascular system; sometimes only a single one exists; but more commonly they are greatly multiplied. Our acquaintance with the circulation in this group, has chiefly resulted from the skilful observations of MM. Milne-Edwards and De Quatrefages.†—In the *Terebella,* whose gills are arborescent, and situated round the head (Fig. 113, *k*, *k*), there lies in the anterior part of the body, on the dorsal aspect, a large trunk (*l*), which receives at its posterior extremity,

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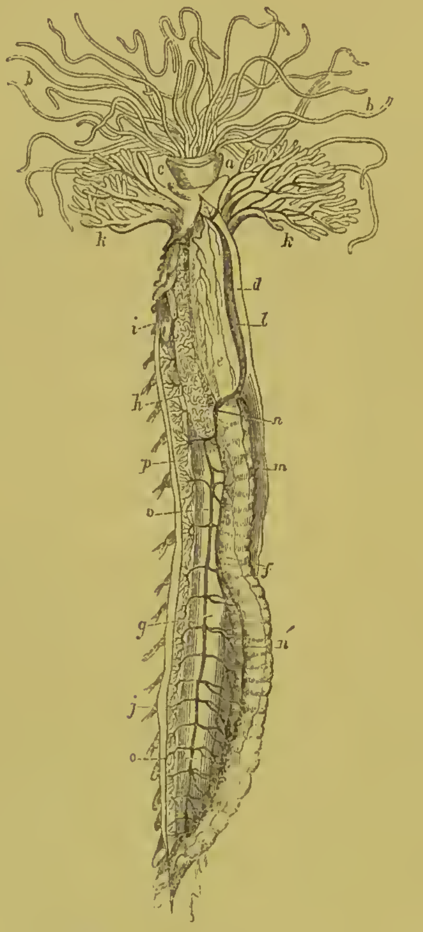
are, it is true, some very cogent objections against ranking the vascular system of the Annelida in the same category; and more especially, the apparent absence of any such external opening, in the neighbourhood of the anus or elsewhere, as is presented by all the ordinary forms of the water-vascular system. But it is by no means certain that such communications do not sometimes exist in the Annelida; and there are undoubted examples among the Entozoa, of vessels which must be ranked as belonging to the water-vascular system, though destitute of any external orifice.—The Author has thought the expression of these doubts to be called-for by the present state of the enquiry, which further research will probably soon elucidate; but he has not felt justified in venturing upon so bold a step as the removal of the supposed sanguiferous system of *Annelida* out of the category of the Circulating Apparatus, although he has felt no hesitation as to this step in the case of the lower Annulose animals.

* This description, which differs from that of M. Dugés, who first described the circulation in the Hirudunidæ, is given on the authority of M. Gratiolet "Ann. des Sci. Nat.," 3e Ser., Zool., Tom. xiv., p. 189.

† See the elaborate Memoir of the former in the "Ann. des Sci. Nat."' 2e Sér., Zool., Tom. x.: and the *résumé* of the researches of the latter already referred to.

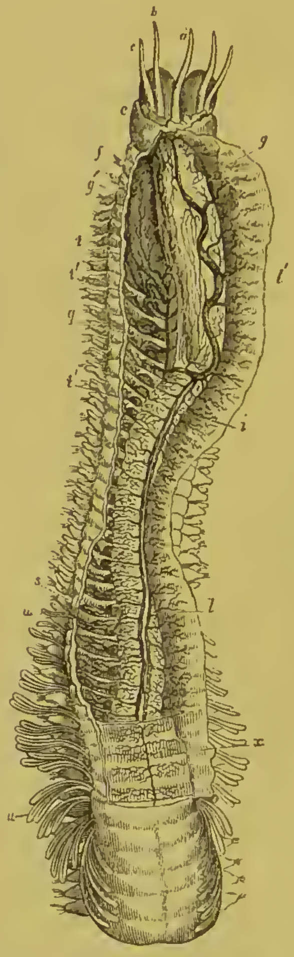
from a venous sinus (n) surrounding the œsophagus, the contents of an extensive vascular plexus, that has ramified on the walls of the intestine,

Fig. 113.



Circulating Apparatus of *Terebella conchilega*:—*a*, labial ring; *b*, *b*, tentacula; *c*, first segment of the trunk; *d*, skin of the back; *e*, pharynx; *f*, intestine; *g*, longitudinal muscles of the inferior surface of the body; *h*, glandular organ (liver?); *i*, organs of generation; *j*, feet; *k*, *k*, branchiæ; *l*, dorsal vessel acting as a respiratory heart; *m*, dorso-intestinal vessel; *n*, venous sinus surrounding œsophagus; *n'*, inferior intestinal vessel; *o*, *o*, ventral trunk; *p*, lateral vascular branches.

Fig. 114.



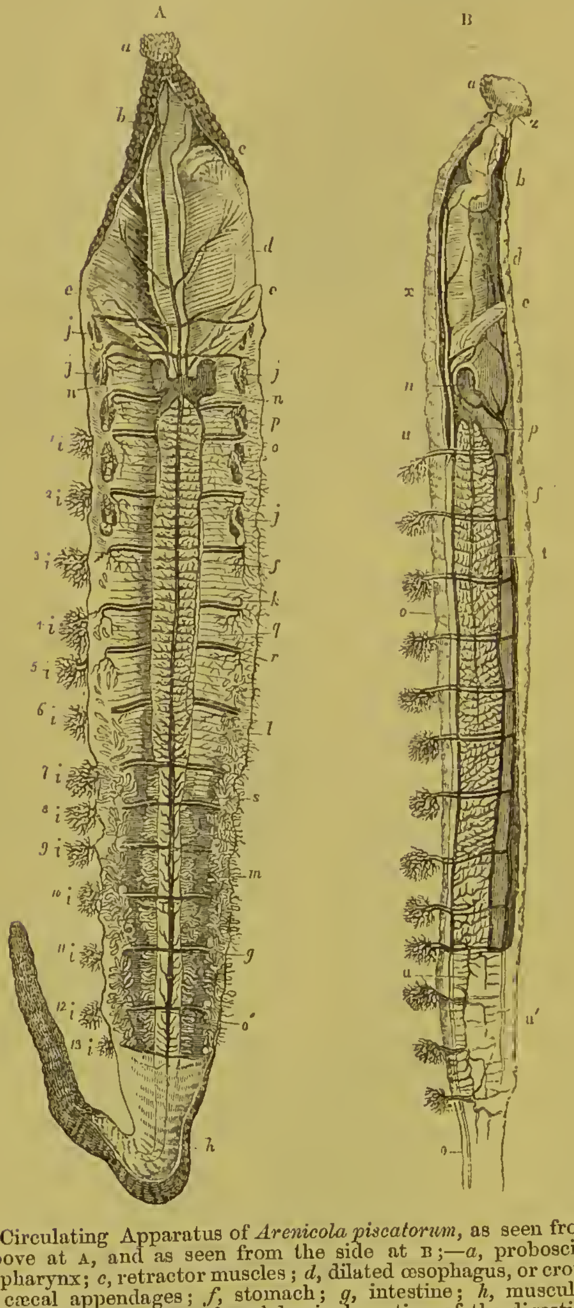
Circulating apparatus of *Eunice sanguinea*:—*a*, *b*, *c*, antennæ; *e*, first segment of the body; *f*, feet; *g*, pharynx; *g'*, mandibular muscles; *i*, intestine; *l'*, dorsal vessel; *l*, superior intestinal vessels; *s*, their lateral branches; *q*, ventral vessel; *t*, its lateral branches; *t'*, contractile bulbs on these branches; *u*, branchiæ; *x*, subcutaneous vessels of the back.

and on the muscles, integuments, &c. This trunk, or dorsal vessel, propels forwards the blood, which it receives from behind, by irregular contractions. At its anterior extremity it subdivides into numerous branches, of which the principal enter the respiratory organs (k, k), whilst others pass to the head and tentacula (b, b); so that a large proportion of the blood is aerated, before it is again circulated through the system. The vessels that return it from the gills reunite into a trunk (o, o), which passes down the ventral surface of the body, giving off a pair of transverse vessels to each segment, and then returning along the inferior side of the intestine (n'); this trunk is of course to be regarded in the light of an artery. The blood is conveyed back into the venous sinus, both from the intestine and from the parietes of the body, by the dorso-intestinal vessels (m), which must be considered as veins. The propulsion of blood into the gills seems principally due to the contractions of the dorsal vessel, which may here be regarded as a sort of respiratory heart; but its motion through the arterial trunk would appear to be partly owing to contractions of the gills themselves, which are occasionally seen to take place. The irregularity of these, however, requires some supplemental force, such as that which has been already described in the inferior tribes, for the maintenance of a steady current; and there are many allied species, in which the blood circulates no less energetically, without any such evident propelling agents.

222. In the *Eunice* (Fig. 114) we find the same general distribution of vessels, but there is an important change in the position in the respiratory organs, which involves a complete alteration in the character of the different parts of the system. The branchial organs (u) are not concentrated round the head, but are disposed in 'combs' along the whole body. The dorsal trunk (l') receives from the dorso-intestinal vessels (l), as in the former case, the blood which has ramified on the intestines; but this fluid, as will presently appear, is as much arterial as venous. The contractions of this trunk are not so regular and powerful as in the Terebella, and seem to be but little concerned in maintaining the circulation. The vessels into which it divides anteriorly, are distributed only to the head and neighbouring parts; and, by the reunion of the vessels which return the blood so distributed, the ventral trunk (q) is formed, which here possesses a venous character. The general distribution of its ramifications is very similar to that described in the Terebella, except that it transmits blood to the branchiæ as well as to the general system; but each transverse branch (t) presents a dilatation or bulb (t') near its origin, which seems to propel the blood that enters it, by regular contractions, partly through the pectinated branchiæ, and partly upon the intestines, cutaneous surface, muscles, &c., after permeating which it re-enters the dorsal vessel. This multiplication of blood-propelling organs is very interesting, when viewed in reference to the general tendency to repetition of parts manifested in this class. It is found that, in the Annelida which possess it, the vitality of portions of the body is preserved during a very long time after the subdivision of the animal. In higher tribes, however, this multiplication is restricted to a particular division of the body, as will be presently seen in the Earth-worm.

223. In the *Arenicola* (Fig. 115) we observe another interesting variety in the arrangement of the vascular system, which partly resembles the forms already noticed, and partly conducts us to others which would at first sight appear entirely different. The dorsal vessel (o, o) traverses almost the entire length of the body posteriorly, and it receives, as before, the blood which has circulated on the intestine and external surface, as well as some directly transmitted by the branchiæ. It terminates, however, at about the anterior fourth of the body, in a kind of contractile ventricle (n), which answers the purpose of a heart; but it first sends forward branches (x) to the head, the vessels returning from which enter the ventral trunk (t)

Fig. 115.



Circulating Apparatus of *Arenicola piscatorum*, as seen from above at A, and as seen from the side at B;—*a*, proboscis; *b*, pharynx; *c*, retractor muscles; *d*, dilated œsophagus, or crop; *e*, cæcal appendages; *f*, stomach; *g*, intestine; *h*, muscular partitions surrounding the abdominal portion of the digestive tube; i^1 to i^{13}, thirteen pairs of branchiæ; *j*, organs of generation; *k*, setiferous tubercles, and their muscles; *l*, secreting cæca of the yellow matter exuded from the skin; *m*, secreting cæca (biliary?) surrounding the intestine; *n*, *n*, heart; *o*, dorsal vessel; *o'*, abdominal portion of the vessel; *p*, lateral intestinal vessels; *q*, subcutaneous vascular network; *r*, branchial arteries and veins; *s*, branchial veins returning to the dorsal vessel; *t*, ventral trunk; *u*, *u'*, cutaneous vessels; *x*, lateral pharyngeal vessels; *z*, labial vascular ring.

that passes backwards from the propelling cavity. The branches of this trunk are almost entirely distributed to the gills (i^1—i^{13}); and the blood which is returned from them, is partly transmitted to the intestine by the lateral intestinal vessels (*p*), partly to the integuments, and partly to the dorsal vessel direct. The branchiæ here, as in the Terebella, seem to exert a direct propelling power on the blood which passes through them.—In the *Lumbricus* or 'Earthworm,' again, we find the dorsal vessel communicating with the ventral trunk, not by *one* contractile cavity at its anterior extremity, but by *several* loop-like dilated canals, which seem to exercise a similar propelling agency. The waves of blood can be distinctly seen, if the animal be kept without food for a time, until it has discharged the black earth which usually fills its intestinal canal. The blood which is thus forcibly propelled into the ventral trunk, is conveyed backwards along the body, and distributed to its different organs, especially to the aquiferous tubes which take the place of the respiratory tracheæ of higher air-breathing Articulata; and from these it is returned to the dorsal vessel, its aeration having been effected through the medium of the general surface.—The great extent and importance of the *capillary system* in the

Annelida, compared with the feebleness of the central propelling powers, is an interesting feature in the character of their vascular apparatus, and shows that we have not yet arrived at a condition of the circulating system very far removed from that which it presents in Plants.

224. In the higher Articulata, the Circulating apparatus, instead of being distinctly differentiated from the 'general cavity of the body,' as it seems to be in the Annelida, is always in intimate connection with it. Through the whole series of Myriapods, Insects, Crustacea, and Arachnida, the 'blood' and the 'fluid of the general cavity' are identical; for the former, in some part of its circulation, escapes into the lacunæ between the tissues, and is diffused through the interior of the peritoneal and pericardiac sacs. And in the embryonic condition of these animals, as in certain degraded forms, the development of whose circulating system is permanently arrested at the same point (§ 231), there is no other circulation than the movement of chylaqueous fluid to and fro within the visceral cavity.—In the Vascular system of the *Myriapoda,* as in other parts of their structure, we meet with the condition which may be regarded as *typical* of the Articulated series; for this class presents the full evolution of that multiple heart, which is developed (so to speak) out of the principal dorsal trunk usually found in the lower Articulata; whilst it also exhibits that uniformity in its structure, and in the distribution of the vessels proceeding from it, which are obscured in the higher Articulata by the unequal development of the successive segments, and by the specialization of particular organs. This change of type, however, is by no means abrupt. It appears from the researches of Mr. Newport,* to whom we owe the greater part of our knowledge of the vascular system of this class, that in the *Iulidæ,* which form the connecting link between the Myriapods and the higher Annelida, the walls of the dorsal vessel are very thin, and the valvular constrictions between its successive segments, which are formed by reduplications of the muscular tunics, are by no means complete; further, the number of these chambers, which corresponds with that of the movable segments of the body, is very large, being no less in one genus than seventy-five. A greater multiplication even than this, is seen at an early period in the life of the Iulidæ; for each of their movable segments, to which two pairs of legs are attached, is formed by the coalescence of two original segments; and every one of the latter at first possesses its own subdivision of the dorsal trunk, the indications of which are seen, even in the adult animal, in the duplication of the cardiac muscles and of the arterial trunks on each side, whilst the cavities have completely coalesced. It has been observed by Mr. Newport and Dr. T. Williams, that in the larva of *Iulus,* the visceral cavity contains a corpusculated fluid; and this fluid may be seen to perform an oscillatory movement, some days before the pulsations of the dorsal vessel can be detected, and before the tracheal system is developed.—In some of the *Geophilidæ,* the number of distinct chambers is even greater than in the Iulidæ, being no fewer than a hundred and sixty in one species; but the whole apparatus presents a higher type of structure.

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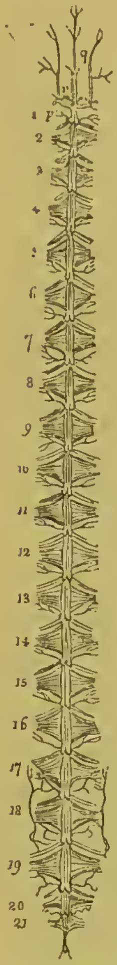
* See his Memoir 'On the Nervous and Circulatory Systems of Myriapoda and Macrourous Arachnida,' in "Philos. Transact.," 1843.

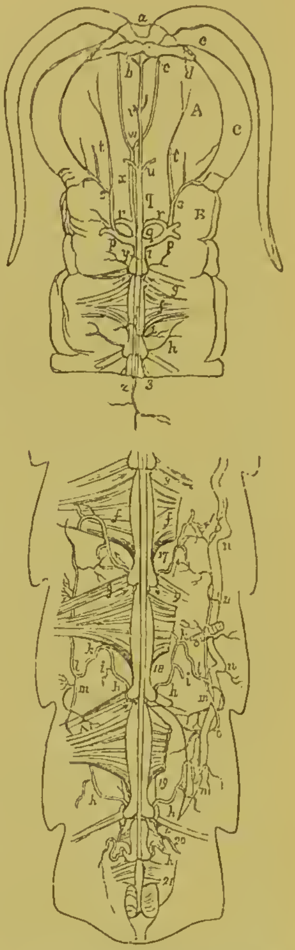
225. In the *Scolopendridæ*, on the other hand, the number of chambers is reduced, in accordance with that of the segments of the body, being never greater than twenty-one (Fig. 116), and sometimes as small as fifteen; the muscular portion of their walls is much more developed; and the valvular partitions which isolate the successive segments from each other, as well as the valves which guard the orifices of the vessels, are much more complete than in the lower tribes. The anterior and posterior portions of this *dorsal vessel*, and the parts in immediate connection with it, are shown in Fig. 117; in which the figures 1, 2, indicate its first and second chambers, and 17, 18, 19, 20, 21, those of the corresponding segments at the opposite extremity. The walls are formed of two layers of muscular fibres, some of them annular and others longitudinal; and similar fibres may be traced upon the principal systemic arteries. The purpose of these fibres is obviously to produce contraction of the chambers; their dilatation being accomplished by the bands of alar fibres, *f*, *f*, which extend to a considerable distance from either side of the dorsal vessel, and are inserted into the dermo-skeleton of their own segment. Each chamber has a pair of apertures guarded by valves, which is probably for the entrance of venous blood; but the source from which they receive it has not been clearly made out; it is probably, however, the great sinus formed by the pericardial sac which surrounds the dorsal vessel. From each chamber, also, a pair of systemic arteries, *h*, *h*, is given off, which are especially distributed to the organs of the upper side of their own segment, but inosculate with those of other segments. From the most anterior chamber (1) is given off a pair of large arches, *p r*, *p r*, which encircle the œsophagus, to meet again upon its under-side in the ventral trunk, *x y;* but it also sends forwards a median trunk

Fig. 116.



Dorsal vessel of *Scolopendra*, composed of twenty-one segments, with its alar fibres.

Fig. 117.



Circulating Apparatus of *Scolopendra:*—A, cephalic segment; B, basilar segment; C, foot-jaws; 1, 2, 3, anterior cardiac chambers; 17, 18, 19, 20, 21, cardiac chambers of the posterior extremity of the body; *a*, antennæ; *b*, *c*, cephalic ganglia; *d*, eyes; *e*, extremity of foot-jaws; *f*, *f*, alar muscles; *g*, *g*, valvular partitions; *h*, *h*, systemic arteries; *i*, *k*, *l*, *m*, *n*, their subdivisions, some of them inosculating with the hepatic vessels *o;* *p*, *p*, aortic arches; *q*, median trunk, continued from the dorsal vessel; *r*, *r*, aortic arches reuniting, to form the ventral trunk; *s*, mandibular artery; *t*, cephalic artery; *u*, *v*, secondary arches; *w*, anterior continuation of the ventral trunk *x*, *y;* *z*, nutrient arteries of the dorsal vessel.

q, that gives off two smaller pairs or arches, *u*, *v*, which in like manner, meet in the anterior continuation of the ventral trunk, *w*. From the median trunk are also given off the vessels which supply the cephalic segment and its organs of sensation; the lateral branches, *s*, *t*, which supply the mouth and its appendages, being furnished by a trunk that comes off from the principal aortic arch on each side. The distribution of the arterial branches of the dorsal vessel is extremely minute; even its own parietes being furnished with distinct nutrient branches, *z*. The *ventral* trunk, which lies upon the ganglionic cord, and is principally formed by the union of the arches that surround the œsophagus, may be regarded as representing the 'aorta' of Vertebrated animals; it is of large diameter in the anterior portion of the body, but gives off a pair of arterial branches in each segment; but at its posterior extremity it is reduced to a comparatively small size, there subdividing into two principal branches, which supply the last pair of legs. The branches successively given off from this aortic trunk chiefly proceed to the muscles of the legs; but one set of them is distributed to the tracheæ; and it is worthy of note that the tracheæ and blood-vessels are mixed-up together in a remarkably intricate manner in the peritoneal membrane.—The course of the blood has not been fully made out; but there is a strong probability from analogy that the venous system is altogether *lacunar;* and that the blood which has circulated through the system, together with that which has been sent to the tracheæ for aeration, finds its way to the great pericardiac sinus, and thence re-enters the dorsal vessel through the apertures in its successive chambers. A portion of this mixed fluid will be at once sent outwards by the contraction of each chamber, into the arterial trunks proceeding from it; but the principal portion will be transmitted from behind forwards by the peristaltic action of the chambers, those of the anterior segments dilating whilst those of the posterior contract; and thus the current will be directed through the aortic arches into the ventral trunk, and also through the arterial branches supplying the head. Besides the dorsal and ventral trunks, we find a pair of *lateral* trunks, *o*, which are specially connected with the hepatic organs; the branches of these inosculate with those of the ventral trunk; but in what way the blood is propelled through them is unknown.—In the family of *Scutigeridæ*, an interesting transition is presented to the structure which the dorsal vessel possesses in Insects; for every alternate chamber is much smaller and shorter than the one before and behind it, and receives very little blood from its auricular orifices, so that, the total number of chambers being sixteen, the number of the principal chambers is no more than eight; whilst at the same time, the whole organ is shorter and of more compact form.

226. It is not a little remarkable that *Insects* should have been long regarded as unpossessed of a proper circulation; the peculiar provision for the conveyance of air through the interior of their bodies having been supposed to render the movement of blood unnecessary. Such, however, is by no means the case; for the circulation in Insects is at least as active as it is in other Articulata; and it is only such an extraordinary rapidity in the flow of blood, as would have been required by animals of such wonderful energy, if their respiration had been localised in one organ, which is rendered unnecessary by the universal diffusion

of that function.—We find in Insects a *dorsal vessel* (Fig. 57, *a a*), formed upon the same plan as that of Myriapoda; but the division into chambers is restricted to the abdominal portion of the body, the vessel being continued through the thorax to the head, as a simple contractile trunk. Thus it happens that the number of distinct chambers never exceeds eight; and it appears that in many Insects it is even less. The muscular walls of these chambers are considerably developed, and their valvular apparatus is very complete. The dorsal vessel is surrounded, as in Myriapoda, with a pericardial sac, in which blood has been seen to move; this may, therefore, be regarded as a venous sinus, from which the blood is received into the several chambers, by a pair of valvular orifices within each. The fluid is propelled from behind forwards, through the successive chambers; and is then driven onwards to the head, through the trunk which is the anterior continuation of them. Several branches have been detected, into which this subdivides for the supply of blood to the parts of the head: but no pair of aortic arches for the conveyance of blood to the under side of the body, has yet been made out, although a ventral trunk has been discovered by Mr. Newport, lying upon the gangliated nervous column, as in Myriapoda. The course of the circulation has been chiefly watched in transparent Larvæ, and in Pupæ during their development; and it has appeared as if, when the currents had once passed out of the dorsal vessel, they made their way rather through lacunæ among the tissues, than through distinct vessels. The principal stream of blood from before backwards does not seem to flow along the ventral trunk, but through two lateral passages which lie near the ventral surface; and it is from these that the secondary currents diverge, which pass into the wings and legs, and then return back to the main stream. These currents, too, seem to be rather 'lacunar,' than restrained by distinct parietes; but it is probable that the walls of the passages may be more complete in the perfect Insect.—The mode in which the aeration of the blood is provided-for in Insects, was long misapprehended; but from the enquiries of M. Blanchard it appears that the tracheæ are ensheathed, even to their minutest ramifications, by prolongations of the sanguiferous canals, and that the blood is therefore aerated wherever the tracheæ penetrate.* This view is in perfect accordance with the fact long since observed by Mr. Bowerbank† and others, that the current of blood in the 'nerves' of the wings moves in a space which completely surrounds the tracheæ.—So far, then, as the course of the circulation in Insects is yet known, it may be probably considered to be as follows. The blood impelled forwards by the dorsal vessel, is transmitted to different parts of the body, either by distinct vessels, or by lacunæ; after passing through the tissues, it finds its way by imbibition into the outer sheaths of the smaller tracheæ, which thus serve to collect it for aeration; and from these it is transmitted, whilst undergoing exposure to the air contained in the tracheæ, towards their external orifices, where it is collected from their sheaths by a system of canals which convey it back into the great pericardiac sinus, whence it enters the dorsal vessel.

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* "Ann. des Sci. Nat.," 3e Sér., Zool., Tom. ix., xii. Such, at least, appears to the Author to be the most probable interpretation of the facts ascertained by M. Blanchard's injections, taken in connection with those observed in the living Animal.—The statements of M. Blanchard have been called in question by several Anatomists, more especially by M. Jolly (Op. cit. Tom. xii.); they have been confirmed, however, by others (Op. cit., Tom. xv.) See also the observations of Dr. T. Williams ("Ann. of Nat. Hist.," Vol. xiii., p. 194), who states that those minute ramifications of the tracheæ, in which the spiral fibre disappears (§ 302) are not accompanied by blood-channels.

† "Entomological Magazine," April, 1833, and October, 1836.

227. The dorsal vessel of the *Larva* is far less perfect in its structure, than is that of the Imago; being sometimes almost as destitute of valvular partitions as is that of the Annelida, and very commonly presenting no higher a development than does that of the lower Myriapoda. But in its advance towards the perfect state, a gradual thickening of its walls, and a completion of its valvular partitions, may be noticed; and at the same time the whole organ becomes contracted in length, and presents a more concentrated condition. In many aquatic larvæ, especially of the order *Neuroptera*, there are leaf-like appendages affixed to the tail, in which the circulation may be distinctly seen, the streams passing-off in loops from the main trunks, and entering them again, so as to be conducted to the posterior extremity of the dorsal vessel. Previously to the metamorphosis, the currents cease in these organs; and this is for the most part true also of the currents in the wings, which may be uniformly observed in these organs in the *Pupa* state, but which very seldom continue for any length of time after the last metamorphosis, although they may be frequently seen in individuals that have recently emerged. The cessation of the circulation in the wings is obviously the cause of their complete deficiency in reparative power; no losses of substance in them being ever made good, so that old bees may always be distinguished from young ones by the chipped indented edges of these organs, resulting from the accidental injuries to which they have been subjected.—In certain aquatic larvæ, especially of the *Gnat* tribe, in which the visceral cavity occupies a large part of the body, this may be seen to be in the freest communication with the dorsal vessel, which has not itself any vascular prolongations; and the movement of the blood, which can be easily watched, on account of the multitude of corpuscles which it contains and the transparency of the bodies of these larvæ, appears to take place from behind forwards in the dorsal vessel, and from before backwards in the great venous sinus, without any diverging currents; not only the parietes of the body, but all their contents, being in such immediate relation with the circulating fluid, that no further provision is necessary. In some larvæ whose development is yet less advanced, even the dorsal vessel appears to be wanting, although the fluid of the visceral cavity is in a state of continual oscillatory movement.

228. The Circulating apparatus of the *Arachnida* presents us, at least in the higher forms of the class, with a much greater completeness than that of Insects; and this is especially seen in the addition of a set of vessels that is specially subservient to the aeration of the blood, in accordance with the greater localisation of the respiratory organs themselves. Nevertheless there is no essential departure from the plan of structure already described as prevailing in Myriapods and Insects; and between the higher members of the former class, and the Macrourous Arachnida, such as the *Scorpion*, the conformity in the arrangement of the vascular

system is extremely close. The following are the most important of the facts ascertained by Mr. Newport (loc. cit.), in his minute investigations into the Circulating apparatus of the *Scorpionidæ.*—The *dorsal vessel* runs continuously from the posterior extremity of the tail as far as the cephalo-thorax, and may be described as consisting of a *cardiac* portion (Fig. 118, *h, h,* 1—7) which occupies the abdomen, a dorsal artery, *a,* which is the anterior continuation of this, and a caudal artery, *q, q,* which is its posterior portion. The structure of the cardiac portion, which contains eight chambers (the posterior one, however, being very imperfect), is similar in most respects to that of the dorsal vessel of the higher Myriapods and perfect Insects; but it differs in this, that the valvular partitions between them are much less complete; a difference which probably has reference to the fact, that the cardiac portion has to send a great arterial trunk backwards as well as forwards. The blood enters the cardiac chambers from the surrounding sinus, through the auricular orifices *u, u;* and a portion of it is sent forth again, without being propelled into the adjacent chambers, through the systemic arteries *p, p.* The anterior continuation, or dorsal trunk *a,* passes through the septum *x,* which divides the cephalo-thorax from the abdomen; and soon afterwards gives off a pair of large branches, which pass round the œsophagus, like the aortic

Fig. 118.

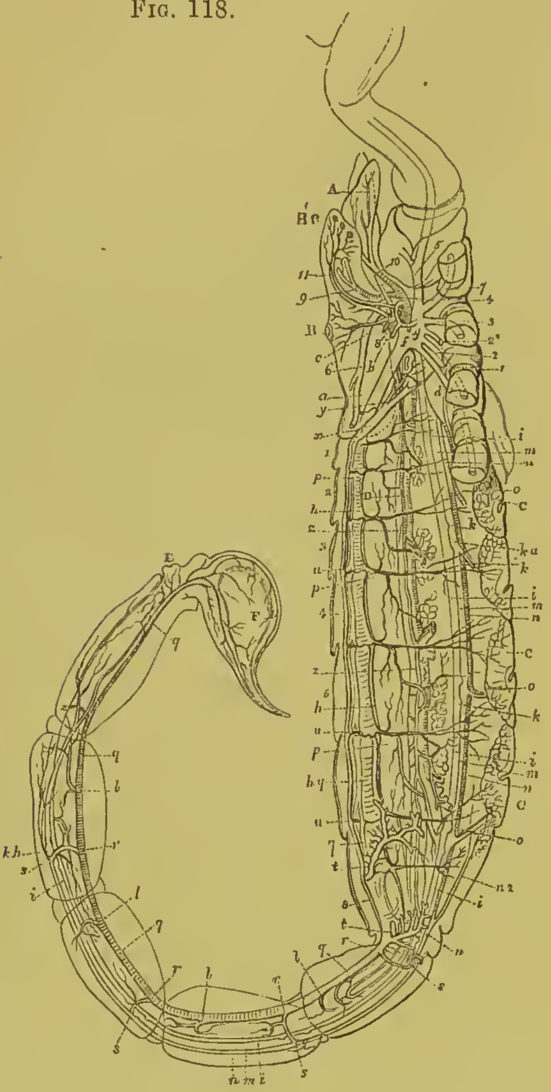
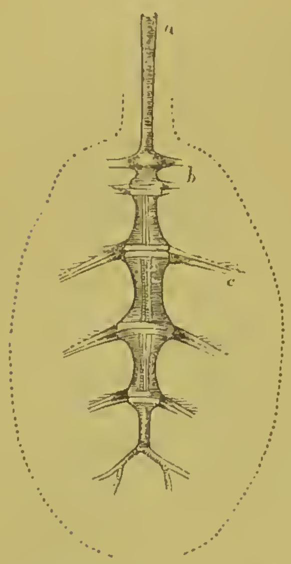


Diagram of the Circulatory and other organs in *Buthus;*—A, antennal claws; B, eyes; C, C, pulmono-branchiæ; D, alimentary canal; E, anal orifice; F, poison-glands; *a,* anterior continuation of the dorsal trunk, giving off 1, 2, 2*, branches to the posterior legs, besides the two great arches which form the ventral trunk; *b,* cephalic ganglia; *c,* optic nerve; *d,* great subœsophageal ganglion; *e,* ocelli; *f,* supra-œsophageal artery, giving off 6—14 branches to the cephalic ganglia and organs of sense; *g,* lateral trunks of subœsophageal arteries, giving off 3, 4, 5, branches to the anterior members; *h, h,* chambers of the heart, 1—7; *i, i,* ventral artery; *k, k,* branches given off in each segment; *l, l,* branches of caudal artery; *m, m,* ganglionic cord; *n, n,* portal system of vessels; *o, o,* its branches; *p, p,* systemic arteries given off from the cardiac chambers; *q, q,* great caudal artery; *r, r,* its branches of communication with the portal trunk *s, s; t,* termination of cardiac portion in anterior dorsal trunk; *u, u,* auricular openings into cardiac chambers; *x,* diaphragm dividing cephalo-thorax from abdomen; *y,* anterior pair of systemic arteries distributed on this; *z,* visceral arteries.

arches of Myriapoda to reunite below it into the ventral trunk *i*, *i*. It then gives off large branches, 1, 2, to the two posterior pairs of legs, and a smaller one, 2*, to the thorax; after which it separates into three principal trunks, of which one, *f*, is median, and runs above the œsophagus, giving off branches (6–14) to the cephalic ganglia and organs of sense, whilst the others, *g*, pass forwards at the sides and below the œsophagus, to supply the two remaining pairs of legs (3, 4) and the great prehensile claws (5). In this arrangement, there is a very marked conformity to the type of the Scolopendra (§ 225). Besides these vessels, the dorsal trunk gives off proper visceral branches, *z*, which proceed backwards along the anterior portion of the alimentary canal, inosculating with branches from the systemic arteries *p*, *p*. The posterior continuation of the multiple heart, constituting the caudal artery *g*, *g*, passes backwards to the extremity of the tail, giving off in its course the systemic arteries *l*, *l*, and also the lateral branches *r*, *r*, which communicate with the portal trunk *s*, *s*.—The *ventral trunk*, *i*, *i*, which lies upon the upper surface of the gangliated nervous cord, extends backwards from its commencement in the aortic arches, nearly to the termination of the tail; gradually diminishing in diameter, as it gives off minute vessels for the nutrition of the cord, and successive pairs of branches, *k*, *k*, which pass downwards to communicate with the portal trunk; its terminal branches in the last caudal segment being distributed with the terminal nerves proceeding from the ganglionic cord.—Beneath the ganglionic column we find another trunk, designated by Mr. Newport as the *portal;* the purpose of which appears to be, to collect the blood from the systemic vessels, and to transmit it for aeration to the pulmonary branchiæ, c, c. This trunk is formed by the coalescence of branches from various sources; but especially from the ventral trunk in the abdominal region, and from the caudal artery in the tail. Its branches are almost entirely distributed upon the respiratory organs.—Such is the general distribution of the proper 'vascular' portion of the circulating apparatus, which seems to be altogether arterial in its character; the venous circulation in the body at large would seem to be altogether 'lacunar;' whilst the return of the blood from the pulmonary branchiæ to the heart probably takes place by definite canals.—The course of the blood, therefore, would seem to be as follows. Of that which is returned from the respiratory organs to the chambers of the multiple heart, one part is sent forth by the systemic trunks proceeding from each chamber which it has just entered, another part is transmitted forwards from chamber to chamber into the dorsal trunk, whilst a third portion seems to be propelled backwards into the caudal trunk. The dorsal trunk distributes the blood to the cephalo-thorax and its organs of sensation and motion; whilst a portion of it is carried backwards through the aortic arches and ventral trunk, partly for the nutrition of the ganglionic cord, and partly for transmission into the portal system. So, again, the caudal trunk conveys the blood backwards to the extremity of the tail, giving off nutrient branches to the various parts of that organ, and also transmitting a part of its contents directly into the portal system. The great portal trunk, (which may perhaps be considered as made up by the coalescence of the two lateral canals that exist in Insects and many Articulata) receiving blood from these sources, and collecting that which has been distributed through the tissues by the systemic branches of the dorsal and ventral trunks, transmits this fluid for aeration to the pulmonary branchiæ, from which it is returned by a set of 'branchio-cardiac canals' to the great cavity surrounding the heart.

229. The circulation has not been studied with the same minuteness in the *Araneidæ;* but from the researches of M. Blanchard* it appears that the course of the blood is essentially the same as in Insects, but that it is distributed by more perfect vessels. The dorsal vessel forms a multiple heart of four or five chambers in the abdominal region (Fig. 119); but the partitions between these chambers are often scarcely perceptible, so that the cardiac cavity is really single but elongated, as in the Stomapod Crustacea (§ 230). The blood is sent forth from this organ, partly by systemic vessels directly proceeding from its segments, but chiefly by the dorsal trunk (*a*) which forms its anterior continuation; and from this, on its entrance into the cephalo-thorax, numerous branches are given off to the various organs of sensation and motion, and also to the viscera contained in that division of the body. The blood thus distributed through the system is stated by M. Blanchard to find its way to the pulmonary branchiæ by lacunar passages, neither ventral trunk nor a portal system of vessels having been yet made out; and from the respiratory organs it is carried back to the heart by distinct branchio-cardiac canals (*b*, *c*,), which discharge themselves into the several chambers of the multiple heart. The more diffused the respiratory function is rendered, by the prolongation of the pulmonary branchiæ into tracheæ, the more does the circulation resemble that of Insects in the predominance of the lacunar over the vascular type.

FIG. 119.



Heart of *Mygale:*—*a*, arterial trunk proceeding to cephalo-thorax; *b*, vessels of the anterior, and *c*, vessels of posterior pulmonic apparatus.

230. It is among the *Crustacea*, that we find the sanguiferous system presenting the most developed form under which it exists in the Articulated series. In the lower orders, however, the segments of whose bodies are nearly alike throughout, the contractile portion of the dorsal vessel is elongated, and the distribution of its branches is nearly uniform in each segment; but the advance towards a higher type is shown in the order *Stomapoda*, the members of which have usually an elongated fusiform heart, developed as a muscular dilatation of a part of the dorsal vessel, which, towards its anterior and posterior extremities, possesses the character of a sanguiferous trunk. The same is the case also in the *Limulus.* But in the order *Decapoda*, which includes the most elevated forms of this class, we find the heart contracted into a short fleshy sac, possessed of considerable muscular power, and concentrating in itself the propellent force which is diffused in the lower tribes through a large part or the whole length of the dorsal trunk. This organ in the *Lobster* is situated on

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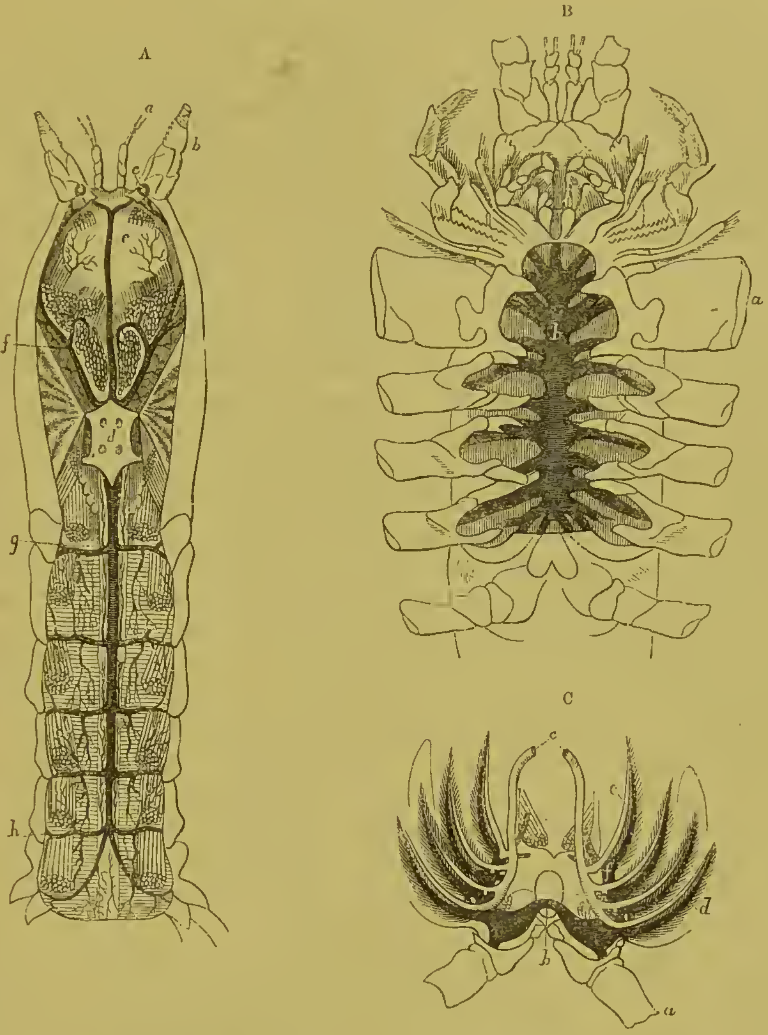
* "Annales des Sciences Naturelles :" 3e Sér., Zool., Tom. xii., p. 317.

the median line, at the posterior part of the cephalo-thorax (Fig. 120, A, *d*); from its anterior part is given-off a large *cephalic* trunk (*e*) which passes

FIG. 120.



Circulating Apparatus of *Lobster*:—A, Heart and Systemic Arteries as seen from above;—*a*, smaller antennæ; *b*, larger antennæ; *c*, eyes; *d*, heart; *e*, ophthalmic artery; *f*, antennar arteries; *g*, *h*, superior abdominal artery.
B, Great Ventral Sinus, receiving venous blood from the system, and transmitting it to branchiæ;—*a*, first pair of legs (claws); *b*, venous sinus.
C, Respiratory Circulation, as seen in a transverse section of one of the segments;—*a*, leg; *b*, venous sinus; *c*, branchio-cardiac trunks; *d*, branchiæ; *e*, branchial veins, or efferent vessels, uniting to form branchio-cardiac trunks; *f*, branchial arteries proceeding from venous sinus.

forwards, and soon subdivides into branches for the supply of the eyes and neighbouring organs, and also a pair of antennary arteries; whilst from its posterior extremity is given-off the abdominal or *caudal* artery (*g*, *h*), from which successive pairs of branches are sent-forth laterally to the segments of the abdomen. The same arrangement prevails in the *Crab* (Fig. 58); but the posterior trunk is there much smaller in proportion, in accordance with the undeveloped state of the abdominal segments. These two trunks, with the heart, obviously represent the entire dorsal vessel of the lower Articulata; the transitional form being shown in the Scorpion. Besides these trunks, a pair of large *hepatic* arteries is given-off from the sides of the heart, which are exclusively distributed to the liver; whilst beneath the caudal artery, a large *sternal* trunk originates, which bends down towards the ventral aspect of the body, where it divides into an anterior and a posterior branch, the former of which supplies the thoracic members, whilst the latter distributes blood to the under surface of the abdomen. This may probably be regarded as homologous with the *ventral* trunk of the Scorpion, though it has not yet been shown to have any connection with the cephalic by aortic arches. The blood conveyed to the body by these arteries, appears to return through the lacunæ of the tissues into two sets of large venous sinuses; of which one consists of a series of flattened cavities, freely communicating with each other, which lies immediately beneath the shell of the back, covering the upper surface of the heart and dorsal trunks, and obviously representing the pericardiac sinus which incloses the dorsal vessel in other Articulata; whilst the other series (*b*, Fig. 120, B, C) lies at the bases of the branchiæ, on each side of the inferior surface of the thorax. The former collects the venous blood from the dorsal and caudal portions of the body, and carries it back to the heart, which it enters by two pairs of orifices, guarded by semilunar valves. The latter (which apparently corresponds to the 'portal' trunk of the Scorpion) collects the venous blood from the maxillæ and legs, and distributes it by branchial arteries (C, *f*) to the branchiæ (*d*) for aeration. From these organs it is again collected by veins (*e*), which all coalesce in a pair of large trunks, the *branchio-cardiac* canals (*c*), that convey the aerated blood back to the heart. Hence, in that central organ, the venous blood received from a portion of the body is mingled with the arterial blood that is transmitted direct from the gills; and the fluid which is propelled through the systemic arteries is hence of a mixed character, as in Reptiles,—a class to which the Crustacea have many points of analogy. Thus the localisation of the respiratory organs in the higher Crustacea, as in Arachnida, involves the existence of a special respiratory circulation.

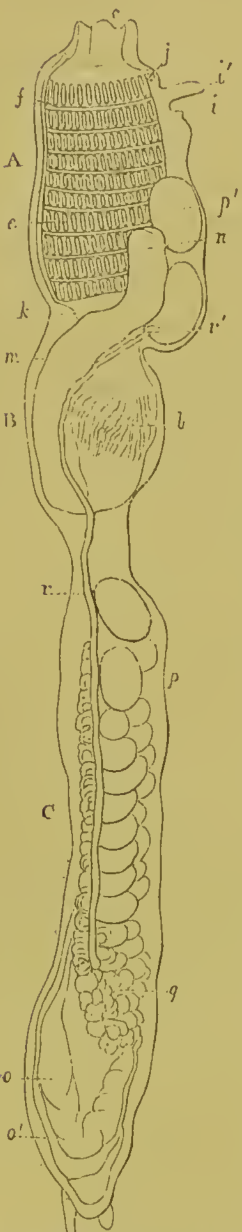
231. In the lower orders, however, the blood is aerated in its progress through the general system, as in Insects; and in many of them, the arterial as well as the venous portion of the system appears to be altogether 'lacunar.' In one of the most degraded forms of the class, we revert to the simplest possible type of the Circulating apparatus; even the dorsal vessel, which is so characteristic of the Articulata, being deficient in the *Pycnogonidæ* (Fig. 105). In these curious animals, there is not the least trace of any vascular system; but the visceral cavity of the body and limbs, that intervenes between the integument with its muscular lining and the stomach with its prolonged cæca, is occupied by a corpusculated fluid, which is kept in a state of continual flux and reflux, not only by the general movements of the body and limbs, but by the peristaltic contractions of the walls of the digestive sac. For when the contraction of the central cavity forces a part of its contents into the gastric cæcum of either of the legs, that cæcum, by its dilatation, presses out a part of the circumambient liquid, which will flow into the cavity of the thorax, whence it may pass into that of any other limb in which space is formed to receive it by the contraction of *its* gastric cæcum.

There is no special organ of respiration; so that the aeration of this fluid through the general integument, in the ordinary course of this strangely-imperfect circulation, must be sufficient for the wants of these inert animals.

232. From the view which has thus been taken of the Circulating apparatus in the higher parts of the *Articulated* series, it will be seen that, notwithstanding the diversity of detail, there is a very general conformity to a definite plan; and that the tendency, as we ascend from below upwards, is to a concentration or specialization in a single organ, of that impulsive power which, in the lower tribes, was diffused through various parts of the system. Now when we follow a similar course with regard to the *Mollusca,* it will be seen that in almost the lowest forms of that series, the central organ is as powerful, and the circulation as much carried-on through distinct vessels, as in the highest Crustacea. The explanation of this general inferiority of the circulating system in the Articulated series is partly to be found, as we have already seen, in the general diffusion of the respiratory apparatus; but it seems to be in part connected with the mechanical arrangements of the body, the continual movements of whose several parts furnish an additional means of propulsion to the blood which is meandering through their lacunar spaces and cavities. Even in Vertebrated animals, we find that the general acts of locomotion have an important share in promoting the flow of blood, especially through the venous system; its trunks being allowed to fill, and being then forced to empty themselves towards the heart (any reflux being prevented by their valves), by the alternate relaxations and contractions of the muscles which are so situated as to press upon them. On the other hand, in the comparatively inert bodies of the Mollusca, the blood would stagnate in its course for want of such assistance, if it were not kept in motion by a powerful force-pump, in the form of a compact heart, with firm muscular walls.—In most of the instances in which we have hitherto found an organ of propulsion materially affecting the current of the circulation, it has transmitted the blood which it has received from the venous sinuses or canals, into the principal 'systemic arteries,' and may therefore be designated as the *systemic ventricle.* Among the Annelida, however, the impelling cavities are frequently situated at the commencement of the branchial vessels, and are to be considered as representing the *pulmonary ventricle* of higher animals. In the *Mollusca* generally, we find, superadded to the ventricle, an *auricle* or contractile cavity, adapted to receive the blood transmitted to the heart, and to propel it into the ventricle; and the existence of these two cavities constitutes the typical character of the heart through nearly the whole of that sub-kingdom, although many variations are presented in their form and situation. Notwithstanding this higher development of the heart, the rest of the circulatory apparatus remains in a state of relative incompleteness; for in the lower classes of this series, the distribution of blood to the general system is almost entirely effected by lacunar spaces, of which the visceral cavity forms part, it being only in the respiratory organs that it moves through distinct vessels; and even in the higher tribes, in which the arterial part of the systemic circulation is generally truly vascular throughout, the venous portion of it is still in some degree lacunar.

233. In the *Bryozoa* there is no other circulation than the flux and reflux of the nutritive fluid, which has transuded through the walls of the alimentary canal into the visceral cavity, whence it passes into the tentacula; a continual movement being kept-up by the peristaltic contractions of the alimentary canal (as in the Pycnogonidæ, § 231), and by the alterations in the form of the visceral sac, consequent upon the retraction or projection of their polypoid bodies. The visceral cavities of the several 'zooids' that have originated by gemmation from the same stock, seem to retain their connection with each other, although this is sometimes narrowed and prolonged so as to form but a slender tube. The stony walls of the 'cells' which invest the soft bodies of many species of *Eschara*, *Lepralia*, &c., are marked with punctations, which are in reality the orifices of short passages extending into them from their internal cavity; and these passages are occupied by prolongations of the visceral sac, which thus convey the nutrient fluid into the substance of the framework formed by the aggregation of the calcified tunics of these animals.

FIG. 121.



Anatomy of *Amaroucium proliferum*:—A, thorax; B, abdomen; C, post-abdomen;—*c*, oral orifice; *e*, branchial sac; *f*, thoracic sinus; *i*, anal orifice; *i'*, projection overhanging it; *j*, nervous ganglion; *k*, œsophagus; *l*, stomach surrounded by biliary tubuli; *m*, intestine; *n*, termination of intestine in cloaca; *o*, heart; *o'*, pericardium; *p*, ovarium; *p'*, egg ready to escape; *q*, testis; *r*, spermatic canal; *r'*, termination of this canal in the cloaca.

234. Although, in the *Tunicata*, we find a special provision for the regular circulation of nutritive fluid, yet this is not very far removed from the simpler arrangement which suffices in the Bryozoa; for the system of passages in which that fluid moves, might be considered as an offset from the general cavity of the body, which still forms an important part of the circuit.—We here find a distinct heart, usually of a somewhat elongated form, and generally situated in the neighbourhood of the ovarium; it is, however, merely a portion of the sinus-system furnished with muscular parietes, and it is not yet divided into auricular and ventricular cavities. In the long-bodied *Polyclinians*, the heart is situated at the extremity of the post-abdomen (Fig. 121, *o*); but in the *Botryllians* (Fig. 51), which have no proper abdominal cavity, it is brought into much closer approximation with the branchial sac; and in the *Salpæ* it holds nearly the same relative position (Fig. 122, A, *e*). In the solitary *Ascidians*, however, it usually lies between the branchial sac and the ventral surface of the body, partly excavated in the muscular tunic. In the curious genus *Pelonaia*,*—which in its general form and in some parts of its structure exhibits an obvious approximation to the Sipunculida, as also (in common with that group) to the Annulose type,—there

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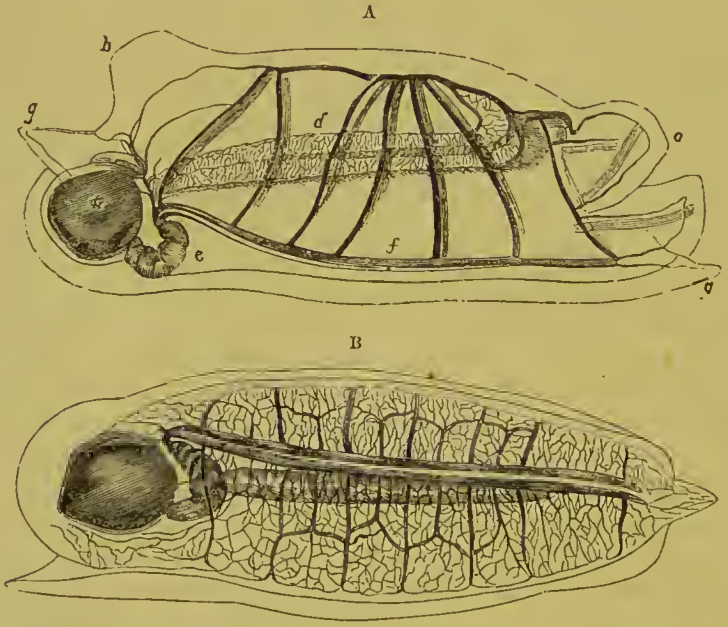
* See Messrs. Forbes and Goodsir, in "Edinb. New Philos. Journ." Vol. xxxi. p. 29.

seems to be no heart, although the vascular portion of the circulating apparatus is more complete than usual; but it is not improbable that the dorsal trunk is contractile throughout, and supplies the place of that organ. The blood does not ordinarily seem to move, in any part of its course, through proper *vessels* with distinct parietes; but flows through a system of *sinuses*, which are in free communication with the general cavity of the body, and which occupy the whole space between the second and third tunics, save where these are adherent to each other. There is usually a principal sinus on the dorsal, and another on the ventral aspect of the body; and these communicate with each other by an intermediate network of channels, which are very close and minute in some tribes, but much wider apart, as well as larger, in others. From this sinus-system, prolongations extend into the 'test' of many species in which this envelope is of considerable thickness; a fact of much interest in its relations to the analogous prolongation of the visceral cavity into the stony cell-walls of the Bryozoa (§ 233), and to that of the sinus-system into the shells of many Brachiopoda (§ 236, *note*).—The most curious feature in the action of the Circulating apparatus in this group, is the *alternation* which presents itself in the direction of the flow of blood; for this renders it impossible to designate either set of vessels or passages as arterial or venous, since both are arterial, and both venous, in their turns. The contraction of the heart, in all the species which are sufficiently translucent to allow it to be observed during life, is somewhat peristaltic in its character, proceeding from one extremity of its cavity towards the other; after the pulsations have continued in either direction for a minute or two, a short intermission takes place, during which the current of blood comes to a stand; and the peristaltic contraction then recommences in the opposite direction, the flow of blood being now first directed towards those parts from which it had last returned. If the course of the circulation be watched in an individual of *Amaroucium* separated from the common envelope, it will be seen that the blood when propelled towards the thorax, passes through the space left between the viscera and the lining membrane of the cavity; chiefly, however, along either its dorsal or its ventral aspect. When the ascending current takes the latter direction (which corresponds to its course in the higher Acephala), it enters a large vertical canal, which is designated as the great 'thoracic' or 'ventral' sinus. From this sinus, a great number of vessels pass off transversely around the branchial sac; and these are connected together by numerous communicating twigs, which pass between the branchial fissures: so that a minute network is thus formed, in which the blood is exposed for aeration to the water that enters the sac. From this network the aerated blood is collected into the 'dorsal' sinus, which also receives blood that has been transmitted to it direct from the thoracic sinus, by means of a vessel that passes round the branchial orifice; so that the fluid which it contains is of a mixed character. From the dorsal sinus the blood returns to the heart, bathing the viscera in its course. When the reversal of the circulation takes place, the blood is first transmitted along the dorsal side of the body to the dorsal sinus; thence it is distributed over the branchial sac; and it finally returns to the heart by the ventral sinus.

235. The circulation in all the Tunicata is performed upon a plan essentially the same; but its peculiarity in certain compound *Clavellinæ*

deserves a special notice. In the *Perophora* (Fig. 138), the several individuals are not included in a common 'test,' but grow by footstalks from a common 'stolon.' Each of these stalks contains a double channel for the passage of blood, and these channels communicate in the common stem with those proceeding from other individuals; so that a vascular communication exists among them all, and this extends also to the undeveloped buds which sprout forth from the stolons. One of the channels in each peduncle enters the heart of the animal which it supports; and of the blood thus received into the propelling cavity, a great part is transmitted along the ventral canal over the branchial surface, whilst the remainder is distributed to the visceral apparatus and the mantle. Both these currents reunite in the dorsal sinus, which then conducts the blood, not back to the heart again, but into the peduncle, in which it may be seen to flow towards the principal stem. As in other cases, however, a reversal takes place about every two minutes; the blood then flowing *towards* the body in the peduncular channel that communicates with the dorsal sinus, and returning *from* it in that which is continuous with the heart. When one of the animals is separated from its peduncle, the circulation is at first disturbed, but soon regains its usual regularity; a new communication being apparently formed, by which a free passage of blood takes place between the dorsal sinus and the heart.*—In many of the *Salpidæ*, we find a much more complete system of vascular passages, adapted to diffuse the blood over the membrane lining the general cavity, as well as upon the special respiratory organ. From the heart (Fig. 122, A, *e*) proceeds the ventral sinus (*f*), which passes

Fig. 122.



Circulating apparatus of *Salpa maxima*, as seen from the side at A, and from the ventral surface at B;—*a*, oral orifice; *b*, vent; *c*, nucleus, composed of the stomach, liver, &c.; *d*, branchial lamina; *e*, heart, from which proceeds the longitudinal trunk *f*, sending transverse branches across the body; *g*, *g*, projecting parts of the external tunic, serving to unite the different individuals into a chain.

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* See Mr. Lister's Memoir in the "Philosophical Transactions," 1834.

towards the anterior extremity of the body, giving off numerous branches at right angles on either side, from which arise numerous smaller branches, the whole forming a minute net-work over the whole of the dilated branchial cavity (B); whilst a separate set of channels distributes blood to the peculiar membranous fold which projects into its interior. From all these vessels it is collected into the dorsal sinus, which conveys it back to the heart. It is also transmitted through the lacunar spaces which immediately surround the viscera. The same alternation may be witnessed in the direction of the flow, in the Salpæ, as in other Tunicata; but here, as elsewhere, it has been noticed that what may be considered as the *direct* current,—*i. e.* the forward movement of the blood from the heart, along the 'ventral' trunk,—is of much longer duration than the *reverse*, in which the blood is propelled from the heart through the 'dorsal' trunk; the number of pulsations being usually about twice as great for the former as for the latter.

236. In the Bivalve Mollusks we find a more complete system of arterial vessels, and the heart is divided into an auricular and a ventricular cavity; but the venous circulation is carried-on, as in the Tunicata, by a system of sinuses in free communication with the general cavity of the body. In the *Brachiopoda*, which are remarkable for their bilateral symmetry, and for the independence of the organs on the two sides of the median plane, there are two separate and distinct hearts, one for either half of the body. Each has a feebly-muscular ventricle, which propels the blood it receives from the auricle into two arterial trunks; the larger of which distributes it to the two halves of the mantle-lobes nearest the ventricle, the smaller to the viscera and muscles. The pallial arteries terminate at the margin of the mantle in the circum-pallial vein or sinus, from which the blood is returned by large sinuses in the substance of the mantle, that discharges it into a large common sinus at the back part of the visceral chamber. This sinus also receives, from the visceral cavity and its extensions, the blood which has been distributed among the viscera and muscles, by the second arterial trunk proceeding from the ventricle; and it discharges its contents into the auricles of the two hearts, each of which has a wide gaping orifice for its admission.* The

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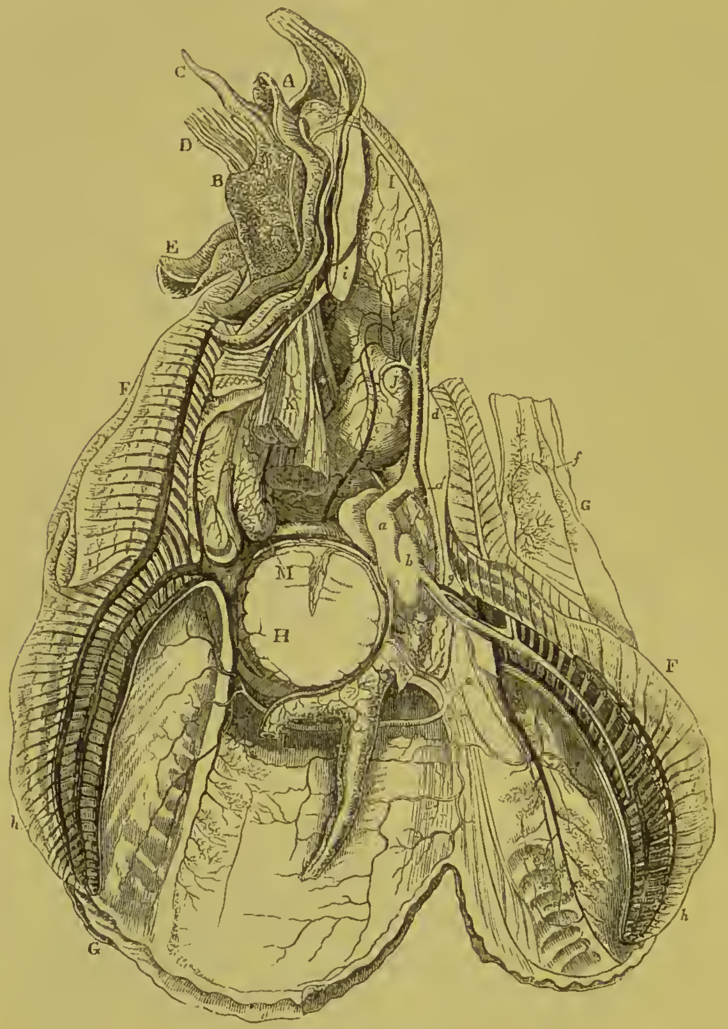
* The account of the Circulating apparatus of Brachiopoda here given, is derived from Prof. Owen's description of the 'Anatomy of the Terebratula' contained in the Introduction to Mr. Davidson's Monograph on the "British Fossil Brachiopoda," published by the Palæontographical Society, 1853.—The Author's own researches have led him to the conclusion, that one very remarkable extension of the sinus-system of Brachiopoda has not been noticed by Prof. Owen. The membrane which can be stripped from the interior of the valves, and which is usually regarded as constituting 'the mantle,' is, in his view, but *one fold* of the mantle; another fold being so incorporated with the inner layer of the shell as not to be distinguishable from it, but being separated by dissolving the calcareous matter with dilute acid. These two layers adhere at many points; and it is to this adhesion that the difficulty of detaching what is commonly regarded as 'the mantle' from the shell, long since noticed by Prof. Owen, is really due; but wherever they do not adhere, the space between them seems to be occupied by blood, which thus fills a capacious sinus-system between the two folds of the mantle, from which are sent, in a large proportion of the Brachiopoda, those curious vascular processes which penetrate the substance of the shell. This sinus-system appears to be strictly comparable to that which intervenes between the second and third tunics of the Tunicata (§ 234); and the vascular processes that penetrate into the shells of Brachiopods correspond with those which extend into the 'test' of that class. See the Author's account of these, in his description of 'The Intimate Structure of the Shells of Brachiopoda,' forming part of the Introduction to Mr. Davidson's Monograph already cited (p. 30.)

pallial portion of the circulation is obviously respiratory, since the blood spread over the extended surface of the mantle is more freely exposed to the aerating fluid, than is that which is distributed elsewhere; and hence the circulation of the Brachiopoda may be compared with that of Reptiles, the aerated blood which has returned from the respiratory surface being mingled in the central cavity with the venous blood which has returned from the system, and a mixed fluid being thus propelled through both the pallial and the visceral arteries.

FIG. 123.



Pinna marina laid open, to show the arrangement of the Circulating Apparatus:—A, mouth; B, foot; C, digitiform appendage to the foot; D, byssus; E, labial tentacula; F, F, branchiæ, those of the right side being in place, those of the left being divided near their anterior extremity, and turned back, so as to expose their anterior surface; G, G, the mantle, of which the left lobe has been detached and folded back; H, posterior adductor muscle; I, first stomach, covered by the liver; K, retractor muscles of the foot; L, anus; M, glandular organ, probably urinary; between this organ and the branchiæ of the right side is seen the second stomach; *a*, aortic ventricle; *a′*, anterior portion of this ventricle, passing round the rectum; *b*, one of the auricles turned back, the other being seen in its natural position on the opposite side of the ventricle; *c*, one of the branchio-cardiac canals; the other is seen in front of the adductor muscle H; *d*, anterior aortic trunk; *e*, posterior aortic trunk; *f*, *f*, pallial veins, proceeding to empty themselves into the branchio-cardiac canals at *g*; *h*, *h*, afferent vessels of the branchiæ; *i*, canal of communication between these last, and the general lacunar system of the abdomen.

237. The chief modification of the foregoing plan in the *Lamelli-*

branchiate Bivalves, consists in the development of a system of branchial vessels; the respiratory function of the mantle being here in great part superseded by the special provision made for it in the lamelliform branchiæ. Although the auricle is still frequently double, there is usually but a single ventricle (Fig. 123, *a*), of which the walls are formed by muscular fibres interlacing in every direction, and even projecting into the interior. From this centre, which is situated between the adductor muscle and the rectum, the blood is sent by two principal arterial trunks, an anterior (*d*) and a posterior (*e*), to the system at large; and thence it is returned, not by distinct veins, but by a system of lacunæ in the substance of the foot (B), of the labial tentacula (E), of the adductor muscle (H), of the glandular organs, and of the viscera generally; the contents of which are collected, in great part by a furrow (*i*) along the free margin of the mantle, into the afferent vessels (*h*, *h*), by which it is conveyed to the branchiæ. After being exposed in these organs to the action of the air contained in the surrounding water, it repasses to the heart by two large branchio-cardiac canals, which do not enter the ventricle, but terminate in auricles (*b*), of which one is usually placed on each side. The branchio-cardiac canals also receive the blood brought back by the venous sinuses from the general surface of the mantle, which still continues to act as a respiratory organ, although the proper branchiæ of the Lamellibranchiate bivalves are undoubtedly the special instruments of this function.*—Although two auricles are found in most Lamellibranchiata, they are not to be regarded as representing the two auricles of air-breathing Vertebrata (§ 245), of which one receives the blood from the system at large, and the other that which is transmitted from the lungs; since here the two auricles have the same function, being both respiratory, and being merely repetitions of one another, separated for the sake of convenience. In the *Oyster*, in fact, they are united into a single cavity; whilst in another tribe, the *Archidæ*, the ventricle is divided like the auricle, in conformity with the breadth of the back of the animal, and the consequent separation of the gills from one another.

238. Among the *Gasteropoda*, we find the same general arrangement of the circulating system; but the situation of its centre, and the distribution of its vessels, present great variation in different orders. The heart (Fig. 124, *h*) is composed of a ventricular and of an auricular sac; the former of which is usually provided with walls of considerable firmness, having muscular bands interwoven with its coats and projecting slightly into its cavity. In some Gasteropoda, as in Conchifera in general, the auricle is double; and in a few genera, even the ventricle is partly divided by the intestine which passes through it. The blood which is propelled from the ventricle by one principal systemic artery, or aorta (*i*), is distributed by its branches (*j*, *k*, *l*) to the various organs of the body; in these it is dispersed through a capillary network possessing distinct parietes; and from this network it passes, not into a proper venous system, but into a set of intercommunicating lacunæ, which even pour it into the visceral cavity (*m*, *m*), so that it bathes the external surface of

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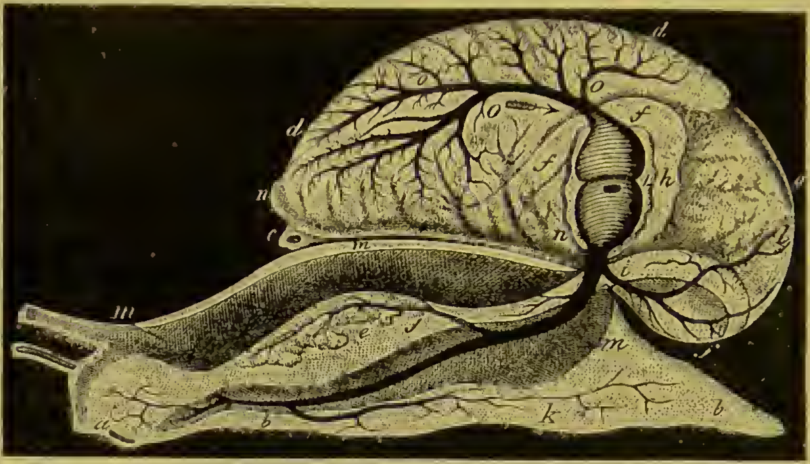
* See the Memoirs of Prof. Milne-Edwards on the 'Circulation in Mollusks,' in the "Ann. des Sci. Nat.," 3e Sér., Zool., Tom. viii., p. 77.

the alimentary canal. From a part of this lacunar system, it is collected into the afferent trunks which distribute it to the respiratory organs whether branchial or pulmonary (*d, d*); and after having been aerated in these, it is returned to the auricle by the branchio-cardiac canals, or pulmonary veins (*o, o*). Into these, however, is also poured the venous blood that is returned by a portion of the lacunar system, without passing through the respiratory organs; so that the general plan of the circulation strongly resembles that which we have seen in the Crustacea (§ 230), only a part of the blood which is sent-forth from the heart, being subjected to the aerating process before returning to it again. The proportion which thus escapes aeration, however, seems to differ considerably in the several orders and genera of the class.—Many curious varieties in the arrangement of the vascular system of Gasteropoda might be enumerated; but it must here suffice to mention that they principally have reference to variations in the condition and position of the respiratory organs, and do not present any essential departures from the type just described. Thus in *Haliotis* and *Patella,* certain parts of the arterial system present the lacunar condition; and in *Tethys,* the branchio-cardiac canals unite into an immense venous sinus, which occupies the dorsal region, and which is only separated from the visceral cavity by a thin membrane.* In *Doris,*† again, the skin appears to act in a considerable degree as a respiratory organ; and the blood which has been distributed to the foot and to the greater number of the viscera, is conveyed, not through the branchial circle, but through a network of vessels in the skin, before returning to the heart; it being only the blood which has traversed the liver, kidneys, and ovaria, that is sent for

Fig. 124.



Anatomy of *Snail:*—*a*, mouth; *b b*, foot; *c*, anus; *d d*, pulmonary sac; *e*, stomach, covered above by salivary glands; *f f*, intestine; *g*, liver; *h*, heart; *i*, aortic trunk; *j*, gastric artery; *k*, artery of foot; *l*, hepatic artery; *m m*, abdominal cavity, serving also as a venous sinus; *n n*, irregular canal communicating with abdominal cavity, and conveying blood to pulmonary sac; *o o*, pulmonary vein, returning blood from pulmonary sac to heart.

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* See Prof. Milne-Edwards's account of the Circulation in these Mollusks, in the Memoirs last referred to.

† See Messrs. Hancock and Embleton's Memoir 'On the Anatomy of Doris,' in "Philos. Transact.," 1852, p. 228.

aeration to the special respiratory apparatus (Fig. 143). In *Eolis*, which has no other respiratory organ than the skin and its papillæ, the blood which has passed through the internal organs finds its way to the surface through an intermediate system of lacunæ; and after being there aerated, is carried back to the heart by branchio-cardiac canals.*—In Gasteropod Mollusks, as in the higher Crustacea, we find the liver very largely developed, and supplied with blood by a large arterial trunk (Fig. 50, *o*). Some yet more special provision for supplying blood to the liver is not unfrequently met-with; the most remarkable at present known being in *Doris*, which has a peculiar contractile cavity, freely communicating with the pericardium (which seems to act as a kind of auricle to it) situated at the commencement of what may be designated the 'portal system' of the liver. Venous blood is returned into the pericardium from the body, without passing through the skin; and this, having been distributed through the liver by vessels proceeding from the 'portal heart,' is collected by a system of more definite veins than are seen elsewhere, and is conducted to the branchial circle, after passing through which, it is returned to the systemic heart. As in higher animals, moreover, the liver is supplied with arterial blood by a branch of the aorta; and this, like the blood of the portal system, is collected by the hepatic veins, and is sent to the branchial circle for aeration.†

239. Hitherto we have usually found the respiratory organs, whether branchial or pulmonary, interposed between the capillaries of the system and the central propelling cavity; the canals which collect the blood from the different organs of the body, uniting only to distribute it again, without any fresh impulse being given to their contents. The only instance of the interposition of anything like an impelling cavity between the systemic and the respiratory vessels, was seen in certain *Annelida*, which are provided with *branchial hearts* (§ 222). Now in Fishes, the heart is entirely respiratory, the arterial trunk which proceeds from it being distributed at once to the gills, and the blood which has been aerated in them being returned into a systemic artery or aorta, whence it proceeds to the body at large; and in the class of *Cephalopoda*, especially in the Dibranchiate order, we meet with a condition of the circulating apparatus, which manifestly establishes the transition between that of the Mollusca in general, and that which is peculiar to Fishes. The *systemic heart* of the *Octopus* consists of only one cavity or ventricle (Fig. 125, *p*), which is usually of a nearly globular form, tolerably strong and muscular, and exhibits on its internal surface bundles of fibres (*carneæ columnæ*) interlacing with one another, as well as distinct valves protecting the orifices by which the blood enters it. The aorta (*q*), and the branches which proceed from it, distribute arterial blood to the general system; and this is returned by means of a regular system of veins possessing distinct parietes, of which one is seen at *r*. Of these, however, one pair

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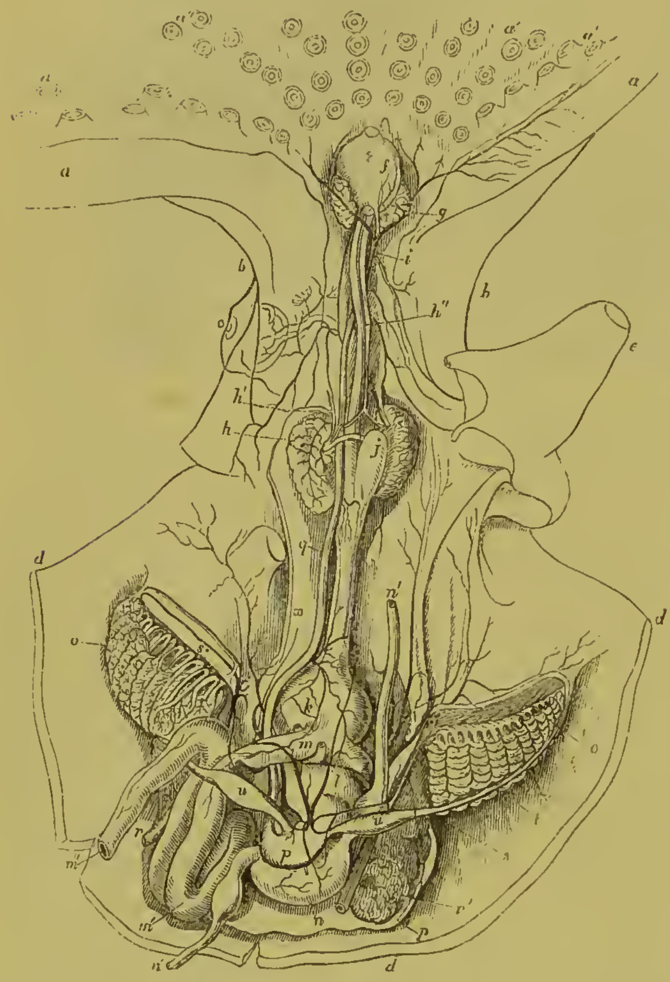
* An attempt was made by M. de Quatrefages, to show that the *Nudibranchiate* Mollusca (Fig. 104) differ from other Gasteropoda in the deficiency of a proper venous system; but this has been negatived, on the one hand, by the discovery that in the Gasteropoda in general the systemic venous circulation is lacunar; whilst, on the other hand, the Nudibranchiata have been proved to possess, like other Gasteropoda, proper branchio-cardiac canals. (See the Anatomy of Eolis, by Messrs. Alder and Hancock, in their Monograph of the "Nudibranchiate Mollusca," published by the Ray Society.)

† Hancock and Embleton, loc. cit.

opens directly into the visceral cavity, which thus, as in the inferior Mollusca, is made to take part in the venous circulation. By the union of the systemic veins on either side, the blood is conveyed, not immediately to the gills, as in the other Mollusca, but to two superadded impelling cavities, or *branchial hearts* (*s*), one of which is situated in connection with each row of gills. These branchial ventricles are less powerful than that which propels the blood through the system; but they are still sufficiently muscular and contractile to accelerate the circulation through the respiratory organs, and thus to prepare the blood for the sustentation of the muscular exertions which are required for the superior locomotive powers of these animals, as well as for the general activity of the functions of their highly-organised bodies. The blood that has been thus impelled through the branchial arteries (*s'*), is returned in an aerated condition by the branchial veins (*t*), which unite into a single branchio-cardiac canal on each side. These canals, before entering the ventricle, present dilatations, (*u*,*u*), which have been usually regarded as mere sinuses; but as they have been observed to be distinctly contractile, they must be considered as in some degree representing the double auricles of the lower Mollusca.—Here, therefore, we find sketched-out, as it were, the complicated form of the vascular system in warm blooded animals

FIG. 125.

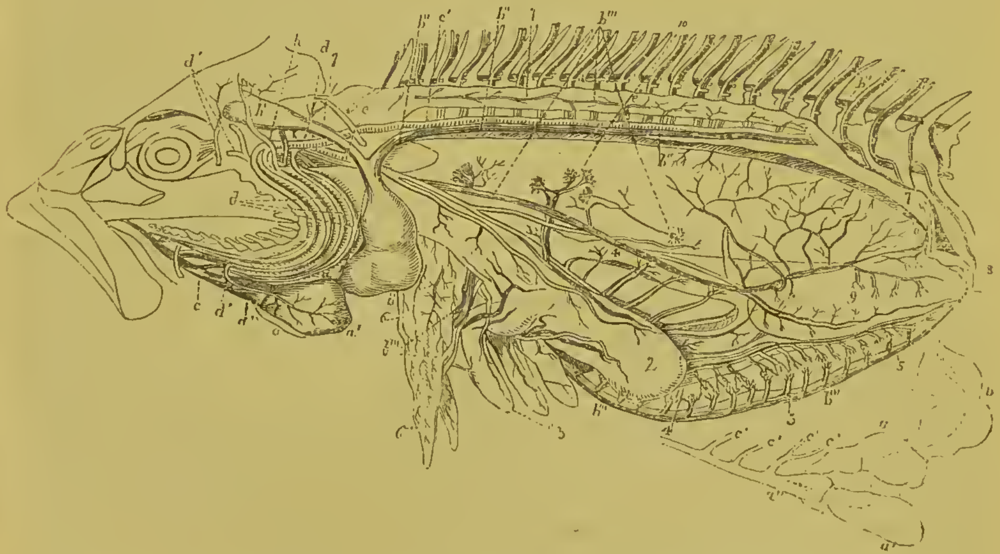


Anatomy of *Octopus*, the animal being laid open on the ventral side, and the inferior wall of the abdominal cavity, with the liver, having been removed:—*a*, *a*, base of the tentacula, with the suckers *a' a'* on their inner surface; *b*, head; *c*, eye; *d*, *d*, mantle turned back; *e*, funnel; *f*, fleshy mass surrounding the mouth; *g*, salivary glands of the first pair; *h*, salivary glands of the second pair, with their suspensory ligaments *h'*, and their excretory canal *h''*; *i*, œsophagus; *j*, crop; *k*, stomach; *l*, spirally convoluted cæcal appendage (rudimentary pancreas?); *m*, commencement of intestinal tube, with biliary canal on each side; *m'*, intestinal convolution; *m''*, anal extremity, turned downwards and to one side; *n*, ovarium; *n'*, *n'*, oviducts, of which the one is in its natural position, and the other turned downwards; *o*, *o*, branchiæ; *p*, heart; *q*, ascending aorta; *r*, venous trunk passing towards the pulmonary heart; *r'*, its glandiform appendage; *s*, pulmonary heart; *s'*, branchial artery; *t*, branchial vein; *u*, *u*, bulbous dilatations of branchio-cardiac veins.

possessed of a complete double circulation; the trunks which convey the blood to the respiratory organs being furnished, like that which distributes it to the system at large, with an impelling cavity, by which a constant and regular current is maintained. In the Tetrabranchiate order, on the other hand, of which the *Nautilus* is the type, the vascular system presents nearly the same arrangement as in the Gasteropoda; for the veins that return the blood from the system enter a common sinus, which has not, however, a distinctly muscular character, and does not seem to possess contractile powers; and from this proceed the four branchial trunks which distribute the blood to the two pairs of gills, whence it is conveyed back to the heart or systemic ventricle by branchio-cardiac canals.—From various parts of the systemic venous trunks, both in the Tetrabranchiate and Dibranchiate orders, a curious series of follicles or little sacs is seen to proceed, forming spongy masses, sometimes of considerable size (Fig. 125, *r′*). The use of these is not certainly known. Their glandular aspect, and the distribution of arterial branches over their surface, joined with the peculiar character of the fluid found in them, have caused them to be regarded as secreting organs, destined to purify the circulating fluid; and it has been thought probable that they are really Kidneys.

240. The complete restriction of the circulating current to the proper vascular system, to which we have seen that the higher Cephalopoda present a near approximation, is one of the typical distinctions of the Vertebrated series, throughout which it universally prevails. For in no

FIG. 126.



Anatomy of the Circulating apparatus and other viscera of a *Fish*;—*a*, auricle; *a′* ventricle; *a″*, bulbous dilatation of the branchial trunk *c*; *b*, sinus venosus; *b′*, trunk and sinus of the cephalic veins; *b″ b″*, great venous trunks from the locomotive organs; *b‴*, venous trunks from the digestive organs, liver, kidneys, generative apparatus, and air-bladder; *c*, branchial artery, giving off a branch to each branchial arch; *d*, branchial veins, whose union forms the aortic trunk that supplies the body with arterial blood, the head and heart being supplied by arteries, *d′ d′*, which originate immediately in the branchial veins; *e*, visceral branch of the aorta; *e′*, spinal trunk, supplying the apparatus of locomotion; 1, œsophagus; 2, stomach; 3, pancreatic cæca; 4, small intestine; 5, large intestine and rectum; 6, liver; 7, renal organs; 8, urinary bladder; 9, organs of generation; 10, swimming bladder.

A, Diagram of the Heart, to show the course of the blood through it; the references as above.

instance does the blood, in any part of its course, escape into the general cavity of the body, or diffuse itself interstitially among the tissues; the introduction of fresh nutrient materials into the circulating current, is no longer accomplished by transudation through the walls of the alimentary canal into the surrounding space, but is effected by absorbent vessels distributed upon its lining membrane (§ 182); and a special system of vessels is also provided for the re-absorption of any superfluous nutritive materials, that may have remained unappropriated by the tissues into which they have transuded from the capillary network (§ 183).—In other respects, we pass from the higher Cephalopods to Fishes without any marked alteration in the type of the Circulating apparatus; save that which is involved in the higher provision here made for the aeration of the blood. The single ventricle of the heart (Fig. 126, *a′*), the cavity of which possesses firm muscular parietes, propels the blood at once to the gills, through an arterial trunk (*c*), which presents a bulbous enlargement (*a″*) at its origin; this *bulbus arteriosus*, as it is termed, will be hereafter shown to exist at an early period of development in the higher Vertebrata, and to conduce towards the formation of the two principal trunks, which are subsequently to arise from the heart (§ 256). This trunk subdivides into four or five branches on each side (A, *c′*, *c′*, *c′*, *c′*), which run along the branchial arches, sending ramifications to every filament. After being thus aerated, the blood is collected by the branchial veins, *d*, into the great systemic artery or *aorta*, which then distributes it to the different organs of the body; and thence it is returned to the auricle by the systemic veins (*b′*, *b″*, *b‴*), which, before entering it, unite in a large dilatation, the *sinus venosus* (*b*).—The circle just described appears simple in character; but it possesses one peculiarity which is worth notice, as foreshadowing more important modifications in higher classes. Two or three small arteries are usually seen passing-off from the branchial arches, so as to convey the pure aerated blood directly to the head, instead of transmitting it to the general systemic trunk. It will be hereafter shown that a similar provision exists in the Crocodile, and has a very important purpose in its economy; and that the same condition is manifested up to the termination of the embryo state of the higher Vertebrata, including the Human species.—Of the blood which is being returned by the veins from the systemic capillaries, a part is diverted into another channel before reaching the heart; for the veins of the digestive and generative organs, together with a part of those proceeding from the posterior part of the body and tail, reunite into trunks which convey the blood to the liver and kidneys; and it is minutely distributed through these organs, in order that it may undergo purification by the elimination of their respective secretions. After this process has taken place, the blood is conveyed to the heart by the hepatic and renal veins, which enter the vena cava, or proceed direct to the sinus venosus. Thus the *portal* circulation, as it is termed, holds precisely the same relation to the general circulation in Fishes, as did the respiratory circulation in the Crustacea and the inferior Mollusca; being interposed, for the purification of the blood which has circulated through the system, between a part of its capillaries and the heart.

241. The foregoing is the general plan upon which the Circulating apparatus of Fishes is constructed; but there are some remarkable de-

partures from it, which requires special notice. The most important of these is that which is presented in the *Amphioxus*, the condition of whose sanguiferous system almost carries us back to the type of *Eunice* (§ 222); for the impelling power is not here concentrated in a single organ, but is distributed among a number of separate pulsatile dilatations developed upon the vascular trunks. Thus we have not only a principal branchial heart (Fig. 127, *ov*), which corresponds in its position to the heart of the

FIG. 127.

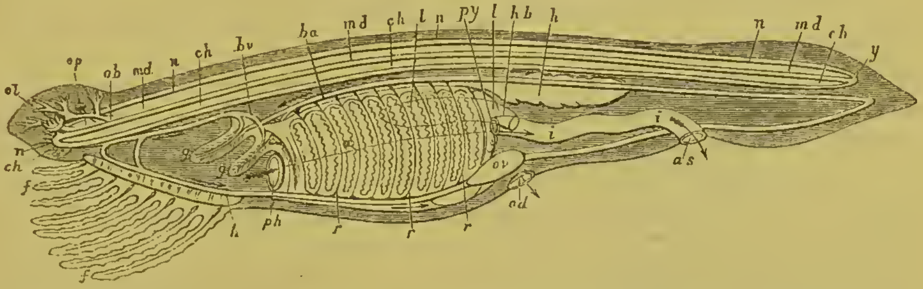


Diagram of the Anatomy of *Amphioxus* or *Branchiostoma* (Lancelet);—*ch*, *ch*, chorda dorsalis; *n*, *n*, fibro-membranous wall of neural canal; *ol*, olfactory capsule; *op*, optic nerve; *ob*, trigeminal nerves; *md*, *md*, neural axis; *bv*, branchial vein; *ba*, branchial artery; *l*, *l*, hepatic cæcum, opening at *hb*; *py*, cardiac orifice; *h*, renal organ; *y*, caudal extremity of neural axis; *as*, anus; *ii*, intestine; *od*, abdominal pore; *ov*, cardiac sinus; *r*, *r*, *r*, dilated œsophagus, with branchial fissures; *ph*, pharyngeal orifice; *g*, *g*, vascular intra-buccal processes; *h*, cartilaginous arch, supporting *f*, *f*, the ciliated labial tentacula.

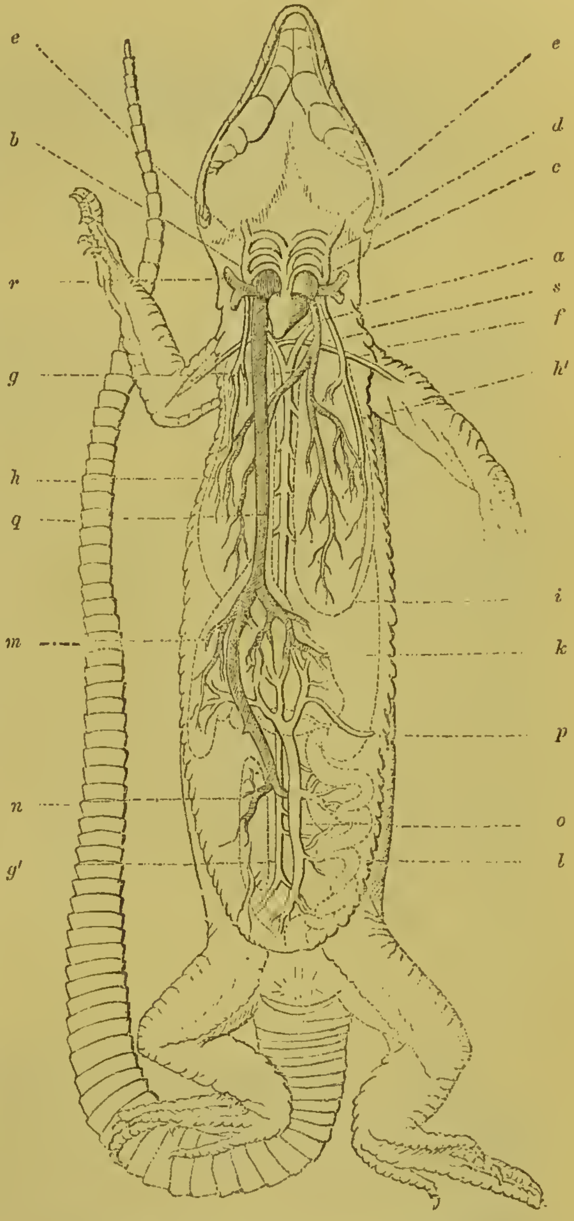
higher Fishes; but there is also a minute contractile bulb at the origin of each branchial artery, so that there are from twenty-five to fifty of these bulbs on either side. The arterial arches, also, at the anterior extremity of the body, appear to be contractile. The venous system, too, is furnished with its own pulsatile dilatations; for a venous heart is developed upon the vena cava or great dorsal vein, and another upon the trunk of the vena portæ, which runs along the ventral side of the intestine.—Some traces of a similar arrangement may be seen in other Fishes, especially in those of the Cartilaginous group. Thus in *Myxine* there is a portal heart, which contracts regularly, and assists in maintaining the portal circulation; in *Chimæra*, which has no bulbus arteriosus, each of the pair of large arteries given off from the aorta to the pectoral fins, has a contractile bulb at its origin; and a pulsating dilatation is found at the extremity of the tail of the *Eel*, where it receives the blood from the delicate veins of the end of the caudal fin, and propels it into the caudal vein.—There is another set of modifications, however, in the Circulating apparatus of Fishes, which conducts us towards the Reptilian type. For there are numerous instances in which the filaments on one or more of the branchial arches remain undeveloped; so that the artery of that arch, instead of subdividing into capillaries, carries-on the blood at once into the aorta; and thus the fluid transmitted through that trunk to the system has only in part undergone aeration, the head, however, being always supplied with pure arterial blood from the branchial veins. Concurrently with this change, we find some provision for *atmospheric* respiration; either in the advanced development of the air-bladder into a rudimentary lung, to which air gains access through a tracheal canal, as in the *Lepidosteus* and *Polypterus*, the two existing representatives of the great *Sauroid* family so abundant in the earlier periods of the Earth's history; or in the development of peculiar organs, analogous to these in function, but not homologous in structure, being saccular prolongations of the lining membrane of one of the gill-chambers, such as are found in the *Cuchia*, an eel-like fish of the Ganges, and in some others of the same tribe (§ 307). The blood is sent to these pulmonary organs by prolongations of the branchial arteries, and is returned from them in an aerated state into the aorta. In some of the Fishes whose Reptilian affinities are the greatest, there is a slight indication of that subdivision of the bulbus arteriosus into two distinct trunks, which takes place during the development of higher animals (§ 258).

242. Quitting now those classes which are modified for existing in water, and passing-on to the air-breathing Vertebrata, we find that very important modifications of the Circulating system are necessary, to adapt these animals to the conditions of atmospheric respiration. It is evident that the blood will be aerated much more rapidly when exposed to the air itself, than when merely submitted to the small quantity which is diffused through the watery element. If, therefore, the whole amount of the circulating fluid be thus exposed, the changes which it undergoes will be performed with such increased energy, that, if the other vital processes be made to conform to them, a 'warm-blooded' animal is produced at once. But as *Reptiles* are intended to lead a life of comparative inertness, and to exist in circumstances which would be fatal to animals of higher organization, the respiratory process is reduced in amount, by the peculiar arrangement of the sanguiferous system now to be described. The ventricle of the heart is either single (which is the case in *Batrachia*) or it is divided by an imperfect septum (as in most of the higher orders), so that the blood which is poured into it from its two sides can mingle more or less freely in its cavity. From this ventricle (Fig. 128, *a*) a single *truncus arteriosus* is given off, which distributes the blood, by a series of arches (*d, d'*) very closely resembling the branchial arches of Fish,—partly to the system, through the cephalic and brachial arteries (*e, f*) which come off from the first and second branchial arches, and through the aorta (*g, g'*) which is formed by the union of the second pair with branches from the third,—and partly to the lungs through the pulmonary arteries (*h, h'*). In some of the higher Reptiles, the pulmonary and systemic trunks are kept distinct at their origin, by the division of the 'truncus arteriosus,' the former arising from the right, and the latter from the left side, of the partially-divided ventricular cavity; still the general appearance of branchial arches is preserved; and a part of the blood expelled by each contraction of the ventricle, is sent to supply the requirements of the nutritive system, and a part is separated for aeration. The pure arterialised blood which returns from the lung by the pulmonary veins (*s*) is conveyed to the left auricle (*c*); whilst the venous blood which is transmitted by the systemic veins (*q, r*) enters the right (*b*); hence these two auricles are not repetitions of one another, but have distinct functions. Both empty themselves into the ventricle, in which the blood derived from these different sources is mixed, and from which one part is again sent to the body, and another transmitted to the lungs (*i*). The portal system of Reptiles corresponds with that of Fishes, in the circumstance that the kidneys are supplied by it with venous blood, as well as the

liver; and also in deriving part of its supply from the veins of the tail, posterior extremities, and genital organs, instead of (as in higher animals) from the veins of the digestive organs alone. The degree in which the renal, hepatic, and portal circulations are united, however, and in which they are supplied from the systemic veins, differs considerably in the several orders; the closest approximation to Fishes being presented (as might be anticipated) in the order Batrachia

243. Although the foregoing may be regarded as the *general* type of the Circulating apparatus in the class of Reptiles, yet there are some very curious modifications of it, some of which connect it very closely with that of Fishes, and others with that of Birds and Mammals. The former are shown in the several genera of *Perennibranchiate Amphibia* (§ 299), which present us with a very complete series of transitional forms connecting the two classes; and also in the progress of the metamorphosis of the *Batrachia,* which in their tadpole or larva condition must be regarded as Fishes in every essential particular of their organization. Their circulation is for a time performed exactly upon the same plan as in that class; the blood being transmitted from the simple bilocular heart to the branchial arches, then being propelled through the branchial filaments, and after aeration being circulated through the system. The mode in which the transition is effected from this condition of the vascular organs, to that which they present in the perfect Reptile state

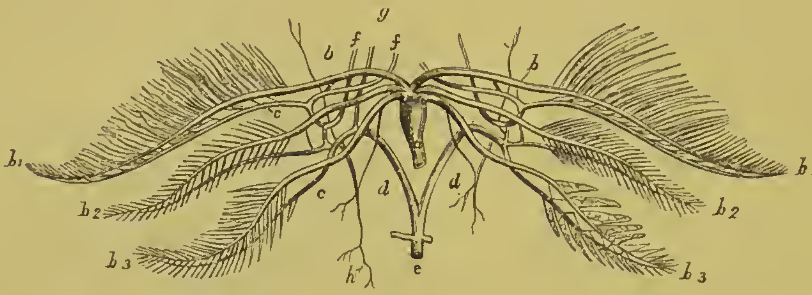
Fig. 128.



Circulating Apparatus of *Lizard*:—*a*, single ventricle; *b*, right auricle; *c*, left auricle; *d d'*, right and left aortic arches; *e*, carotid artery; *f*, brachial artery; *g*, *g'*, ventral aorta; *h*, *h'*, pulmonary arteries; *i*, lung; *k*, stomach; *l*, intestine; *m*, liver; *n*, kidney: *o*, vena portæ; *p*, gastric vein; *q*, vena cava ascendens; *r*, vena cava descendens; *s*, pulmonary veins.

of the animal, described in the preceding paragraph, will be rendered intelligible by the accompanying figures. In Fig. 129 is seen the arrangement

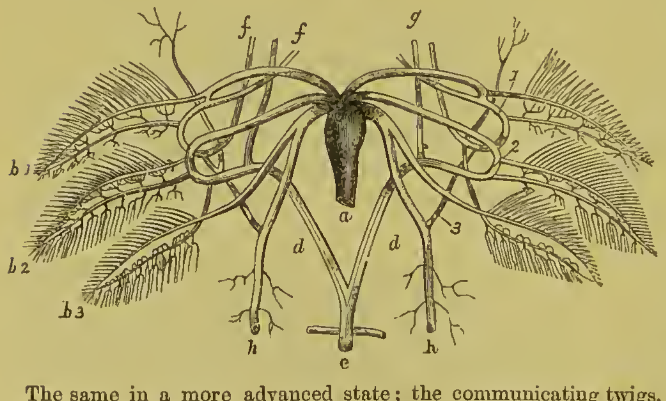
Fig. 129.



Respiratory Circulation of the *Tadpole* in its first state:—*a*, arterial bulb, giving off three pairs of branchial arteries, *b*, to supply the gills, b^1, b^2, b^3, from which return the branchial veins, *c c*; by the union of the second and third of these are formed the two arches, *d d*, which coalesce to form the aortic trunk *e*; from the first pair are given off the cephalic arteries, *f*, *f*; and another trunk, *g*, is derived on each side from the aortic arch; *h*, *h*, pulmonary arteries as yet rudimentary; between the branchial arteries and their respective veins, at the base of the gills, are minute inosculating twigs, the position of which is better seen in the succeeding figures.

of the parts before the metamorphosis has commenced. Three branchial trunks (*b*) pass off on each side of the heart, terminating in a minute capillary network which is contained in the branchial arches (b^1, b^2, b^3), and by which the blood is aerated during the aquatic existence of the animal; from this network the returning vessels take their origin, which unite into trunks (*c*, *c*), one for each gill; and of these the first gives off the main arteries (*f*, *f*) to the head, while the second and third unite into the two trunks (*d*, *d*) which coalesce to form the great systemic artery (*e*), as in Fishes. But, besides these vessels, there are some small undeveloped branches, which establish a communication between each branchial artery and the returning trunk that corresponds with it. There is also a fourth small trunk given off from the heart, which unites with another small branch from the aorta, to form the pulmonary arteries (*h*, *h*) which are distributed upon the (as yet) rudimentary lungs. After the metamorphosis has begun, however, by which the animal from a Fish has to be converted into a Reptile, the branches (Fig. 130, 1, 2, 3) that connect the arteries of the gills with their returning trunks are much increased in size, so that a large part of the blood flows continuously through them without being sent to the gills at all, and the

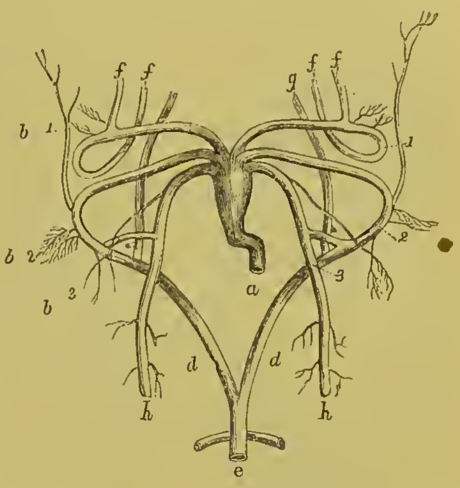
Fig. 130.



The same in a more advanced state; the communicating twigs, 1, 2, 3, as well as the pulmonary arteries, *h*, *h*, being now greatly enlarged in proportion to the branchial vessels.

branchial vessels (b^1, b^2, b^3) are themselves relatively diminished; whilst at the same time, the pulmonary trunks (h, h), which were before the smallest, become the largest, so that an increased proportion of blood is sent to the lungs. By a continuance of these changes, the branchial vessels gradually become obliterated, and the communicating branches, which were at first like secondary or irregular channels, now form part of the continuous line of the circulation (Fig. 131); the upper one sending off the cephalic vessels, the second and third uniting to supply the trunk, and the fourth passing as before to the lungs.—Turning from these to the *Perennibranchiata*, we find in the *Lepidosiren* a plan of circulation but little elevated above that which has been just described as existing in certain Fishes that present approximations to the Reptilian class. The ventricular cavity is single, and gives off but one primary trunk, which is furnished with a 'bulbus arteriosus.' This trunk subdivides into six pairs of branchial arteries; of which the 1st, 4th, 5th, and 6th are distributed to the branchial fringes; whilst the 2nd and 3rd are not thus distributed, their arches having no gills attached to them, but reunite to form the aortic trunk, first giving off, however, the pulmonary arteries. Thus the blood which finds its way into the aorta, consists partly of that which has been aerated in the branchiæ, and partly of that which has passed to it direct from the heart. But that which is transmitted from the heart is itself of mixed quality, as in Reptiles; for the pulmonary vein passes through the systemic auricle, and discharges itself directly into the ventricle, where its aerated blood is mingled with that returned by the systemic veins.—In the *Proteus*, the arrangement of the vascular system permanently resembles that which has been represented as intermediate between the larva and the perfect condition of the Frog. This animal is provided with lungs slightly developed, as well as with permanent gills; and the blood which is expelled from the ventricle is partly transmitted through the gills, partly finds its way directly into the aorta by means of the communicating branches, while a small quantity is transmitted to the lungs; the latter is returned perfectly arterialised to the auricle here developed upon the pulmonary vein, and is afterwards mixed in the ventricle with the venous blood transmitted from the systemic auricle.

FIG. 131.



The same in the perfect *Frog;* the vessels of the branchiæ b^1, b^2, b^3, being now atrophied, the communicating twigs 1, 2, 3, now become the principal channels for the direct passage of the blood from the branchial arteries to the cephalic vessels *f*, *g*, the aortic arches *d*, *d*, and the pulmonary arteries *h*, *h*.

244. In many of the higher Reptiles, on the other hand, we find the cavity of the ventricle more or less perfectly divided into two, and the pulmonary circulation more completely separated from the systemic. Thus, in the *Lacerta ocellata* (spotted lizard), whose ventricle is partly

divided, the right side of it, into which the systemic auricle discharges itself, gives off the pulmonary trunks, so that a large proportion of the venous blood brought back from the system is transmitted to the lungs for aeration; and this being returned to the pulmonary auricle, is discharged into the left side of the ventricle, from which the systemic arteries proceed. As long as there is any direct communication, however, between the two sides of the heart, it is obvious that a part of the blood returned from the systemic veins may be sent immediately into the aortic trunks, without being previously arterialised; whilst in proportion to the degree in which the septum is complete, will be the approach of the animal towards the condition of the warm-blooded Vertebrata. The distribution of the vessels has a considerable effect upon the character of the fluid with which individual organs are supplied; for in Reptiles which manifest this separation to a considerable extent, a part of the blood transmitted to the system has still a venous character, whilst that which is furnished to the brain and upper part of the body is purely arterial. This difference arises from the fact, that of the two arches which unite to form the aortic trunk, one is connected with the right and the other with the left side of the ventricle; the latter receives chiefly the arterial blood from the left or pulmonary auricle, and this gives off branches which convey it without admixture to the head; while the main trunk passes on to unite with the second aortic arch, which arises from the right side of the heart, and which is consequently supplied chiefly with venous blood, that has been brought back from the system into the right auricle. This second arch, before its union with the first, however, gives off a large branch, which is distributed to the intestines and other viscera, and which, therefore, contains venous blood with little admixture of arterial; and the common aortic trunk, formed by the union of the two arches, conveys mixed arterial and venous blood to the remainder of the trunk and members. It is beautiful to observe how by these simple contrivances the greatest economy of material is obtained, whilst each organ is supplied with blood sufficiently oxygenated to maintain its functions.—The *Crocodile* presents us with a condition of the vascular system still more allied to that of warm-blooded Vertebrata; the ventricular septum being complete, and the circulation, as far as the heart is concerned, being truly double. Still, however, whilst the principal aortic trunk arises from the left ventricle, which contains nothing but arterialised blood, a second arch arises from the right (or venous side) along with the pulmonary artery, of which it might almost be considered a branch; and this, after giving off its intestinal branches, enters the first trunk, which has already furnished the cerebral arteries with pure arterial blood, and transmits the mixed fluid to the rest of the system. There is another communication between the trunks arising from the two sides of the heart, by means of an aperture which passes through their adjoining walls just after their origin; so that although the blood in the heart is entirely venous on one side and arterial on the other, it undergoes admixture in the vessels according to the character of the functions to which it is to minister. We shall presently see a remarkable analogy to this distribution of the vascular system, exhibited in the fœtal condition of Birds and Mammals (§ 258).

245. In the highest form of the Circulating system, that possessed by

the 'warm-blooded' Vertebrata, *Birds* and *Mammals*, there is a complete double circulation of the blood; each portion of it, which has passed through the capillaries of the system, being aerated in the lungs, before being again distributed to the body. This is effected by a form of the vascular apparatus, of which a sketch was presented in the *Cephalopoda* (§ 239), and to which a near approach is exhibited by the higher Reptiles. The heart consists of four cavities, two auricles and two ventricles; those of the right or venous side having no direct communication with those of the left or arterial side; and the vessels proceeding from them being entirely distinct, and having no connection whatever, except at their capillary terminations. The blood transmitted by the great veins of the system to the *right* auricle or receiving cavity, passes into the ventricle or propelling cavity, and is transmitted by it through the pulmonary arteries to the lungs of the two sides. After being there arterialised by exposure to the atmosphere, it is brought back to the *left* auricle; and having been poured by it into the corresponding ventricle, is transmitted through the great systemic artery or aorta to the most distant parts of the body (Fig. 132). The heart is therefore completely duplex in structure, and, so far as its functions are concerned, might be regarded as consisting of two distinct portions; for economy of material, however, these are united, the partition between the ventricles serving as the wall to each. In the *Dugong* (one of the aquatic *Pachydermata*), however, the heart is bifid at its apex, and thus presents a partial division into two separate organs, not only functionally but structurally.—The portal circulation is limited in Mammalia to the liver, the kidneys being supplied with arterial blood only. In Birds, however, we find a trace of that arrangement of this peculiar offset from the general circulation, which has been pointed-out as existing in Reptiles and Fishes; for the great portal trunk receives its blood, not only from the veins of the digestive apparatus, as in Mammalia, but also by branches from those of the pelvis and posterior extremities; and it still communicates with the renal circulation, although this connecting branch seems rather destined to convey blood *from* than *towards* the kidney.

FIG. 132.

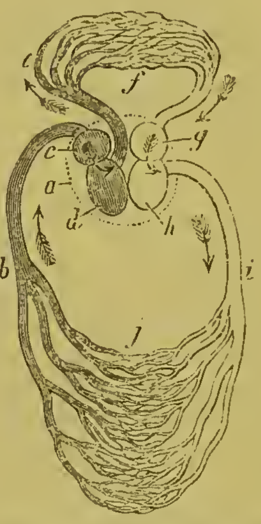


Diagram of the Circulating apparatus in *Mammals* and *Birds*:—*a*, the heart, containing four cavities; *b*, vena cava, delivering venous blood into *c*, the right auricle; *d*, the right ventricle propelling venous blood through *e*, the pulmonary artery, to *f*, the capillaries of the lungs; *g*, the left auricle, receiving the aerated blood from the pulmonary vein, and delivering it to the left ventricle, *h*, which propels it, through the aorta, *i*, to the systemic capillaries, *j*, whence it is collected by the veins, and carried back to the heart through the vena cava, *b*.

246. Various peculiarities in the distribution of the sanguiferous system, which are presented by different orders of Birds and Mammals, would be worthy of notice if our limits permitted. Of these, one of the most remarkable is the modification both of the venous and arterial trunks, existing in the *Cetacea* and other diving animals, which are occasionally prevented from respiring for some time, and in which, therefore, the arterialisation of the blood is checked. Various arteries of the trunk are here found to assume a ramified and convoluted form, so that a large

quantity of blood may be retained in the reservoirs formed by these plexuses; whilst the venous trunks exhibit similar dilatations, capable of being distended with the blood which has been transmitted through the system, so as to prevent the heart from being loaded with the impure fluid, whilst the lungs have not the power of arterialising it. In some diving animals, this object is effected, not so much by a number of venous plexuses, as by a single great dilatation of the vena cava before it enters the heart, resembling the 'sinus venosus' of Fishes.—In other instances, the force with which the blood is sent to particular organs seems to be purposely diminished, by the division of the trunk that conveys it, into a number of smaller vessels, which, after a tortuous course, unite again and are distributed in the usual manner. A structure of this kind is found in the arteries of the long-necked grazing animals, to which the blood would be transmitted with too great an impetus, owing to the additional influence of gravitation, were it not retarded by such a contrivance. A similar distribution of the arteries is found in the trunks supplying the limbs of the Sloths, and of other animals which resemble them in tardiness of movement. In other cases, the arterial canals are specially protected from compression by surrounding organs, in order that there may be no obstruction to the passage of blood through them, and that they may be guarded from injury; thus, in the fore-leg of the Lion, where all possible force and energy is to be attained, the main artery is made to pass through a perforation in the bone, as if to secure it from the pressure of the rigid muscles, which, when in a state of contraction, might otherwise altogether check the current through it. In most Mammals, as in Man, the right anterior extremity is more directly supplied with blood from the aorta than the left; so that the superior strength and activity of this limb would seem to be not altogether the result of habit and education, as some have supposed; in Birds, however, where any inequality in the powers of the two wings would have prevented the necessary regularity in the actions of flight, the aorta gives off its branches to the two sides with perfect equality. Some further peculiarities in the distribution of the arterial system will be hereafter noticed (§ 263).

247. Having now traced the Sanguiferous system to its highest form, it is proper to inquire how far this differs functionally from that simple condition which it presents in the lowest tribes in which it has any distinct existence. There can be no doubt that, in the higher animals possessed of a distinct muscular heart, *this* is the chief agent in keeping-up, by its successive contractions and dilatations, the motion of the blood through the vessels. But a careful survey of all the phenomena of the circulation would seem to lead to the conclusion, that the impulse of the heart is not the *only* means by which the motion of the blood is sustained; but that an additional impulse is given by the contraction of the muscular walls of the arteries, upon the jets of blood successively impelled into them by the heart; and that the changes which this fluid undergoes in the capillaries have some share in its production, and have at any rate a very considerable modifying effect upon the quantity transmitted through the individual organs. We have seen that in Vegetables the laticiferous circulation is entirely capillary; that in the Holothuria there is no central contractile organ which seems powerful enough to impel the blood through

all the minute ramifications of its vascular system; whilst even in the higher Articulata, and in all Mollusca save the Cephalopods, so large a part of the systemic circulation is 'lacunar,' that it seems impossible to imagine that the action of the heart can urge the blood through the branchial vessels which succeed. Some more 'diffused' forces, therefore, would seem to be in operation; and the following are among the facts which appear to support the conclusion, that, even in the highest animals, these most general forces are not obliterated, but are merely superseded by the energy of the special organ, which is developed as the centre of the whole circulation, and which is endowed with an amount of power sufficient to govern and harmonise the numerous actions going-on in different parts of the system.

248. In many warm-blooded Vertebrata, and still more in the cold-blooded Reptiles (amongst which the vitality of individual parts much longer survives injury to the general system), motion of blood in the capillaries has been seen to continue for some time after the heart has ceased to act or has been removed, or after the great vessels have been tied; and this motion may be immediately checked by certain applications to the parts themselves. After most kinds of slow natural death, the arterial trunks and left side of the heart are found to be almost or even completely empty, and the venous cavities to be full of blood.* This effect has been ascribed to the contraction of the arterial tubes after the heart has ceased to beat; but it seems impossible that it can be entirely due to that cause, since their calibre is not found to have diminished in a proportional degree; it must be partly attributed to a continuance of the capillary movement, after the general systemic circulation has ceased. The continuance of various processes of secretion, and even of nutrition, subsequently to general or *somatic* death, affords an excellent proof of this lingering vitality; and it is scarcely possible that these can be maintained without some degree of capillary circulation. There are certain kinds of sudden death, however, in which the vitality of the whole system appears to be simultaneously destroyed, and the blood remains in the vessels as it was at the moment of decease.—Further, a careful examination of the circulation in the living animal discloses many irregularities in the rate of the capillary currents, which it is impossible to attribute to an influence derived from the heart or from the vessels that supply them; and such variations may present themselves, either in the capillary network of a part, or in a portion of it; the circulation taking place with diminished rapidity in one spot, and with increased energy in another, though both are supplied by the same trunk. The change sometimes extends to a complete reversal of the direction of the movement, in certain of the transverse or communicating branches; this movement taking place, of course, from the stronger towards the weaker current: and not unfrequently an entire stagnation, of longer or shorter duration, precedes the alteration of the direction. Irregularities of this kind are most frequent, when the heart's action is enfeebled or partially interrupted; and it

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* It has been observed by Dr. Bennett Dowler, that in the bodies of individuals who have died of yellow fever, the external veins frequently become so distended with blood *within a few minutes* after the cessation of the heart's action, that, when they are opened, the blood flows in a full stream, as in ordinary blood-letting. ("New Orleans Med. and Surg. Journ.," Jan., 1849.)

would thus appear that the local influences by which they are produced, are overcome by the propelling power of the central organ, when this is acting with its full vigour. When the whole current has nearly stagnated, and a fresh impulse from the heart renews it, the movement is seldom uniform through the entire plexus supplied by one trunk; but is much greater in some of the tubes than in others,—the variation being in no degree connected with their size, and being very different in its amount at short intervals.

249. Amongst the most remarkable proofs of the influence of forces generated in the Capillary circulation, on the general distribution of the blood, is one derived from the observation of organs which undergo changes in activity that are quite independent of alterations in the heart's action. Thus, when the uterus begins to develope itself during pregnancy, the unusual activity of its nutritive operations induces an increased demand for blood in its capillary circulation, which is supplied by an increase in the diameter of the trunks that transmit fluid to the organ; and this is entirely independent of any increased energy in the heart's action, which would have affected the whole system alike. The same may be said of the occasional development of the mammæ for the secretion of milk; of the rush of blood through these organs during the act of suckling; and of similar changes in other parts, of which the activity is not constant or uniform. In certain diseased states, also, of particular portions of the system, which do not occasion any appreciable alteration in the heart's action, the quantity of blood sent to the part is much increased, and the pulsation of the arterial trunk leading to it is evidently stronger than that of the corresponding vessels on the outside of the body. These phenomena, and many others which might be mentioned, are evidently analogous to one formerly stated as having been ascertained by experiments on Plants (§ 201); and, when taken in connection, they seem to indicate without much doubt, that the quantity of blood sent to individual organs, and the force with which it is transmitted through them, are augmented with any increase of energy in the vital processes taking place in them, the *vis à tergo* derived from the impulsive power of the heart remaining the same.—Additional evidence of the influence of the forces generated in the capillaries, on the general circulation, is derived from cases in which the normal changes to which the capillary circulation ministers are suspended, and in which it then appears that the heart's impulse is not alone sufficient to maintain the current of blood. One of the most conclusive of these proofs is drawn from the phenomena of *Asphyxia*, or suffocation; since it now seems distinctly ascertained, that the check given to the circulation, and thence to all the other functions, arises from the stagnation of the blood in the capillaries of the lungs, consequent upon the cessation of the reaction between that fluid and the air.* So again, cases of spontaneous gangrene of the lower extremities are by no means of unfrequent occurrence, in which the local stagnation of the circulation has been clearly dependent upon the cessation of the

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* For a fuller discussion of this part of the subject than the limits of this treatise permit, see the Author's "Human Physiology" (§ 575), and his Article on *Asphyxia* in the "Library of Practical Medicine." See also the very conclusive experiments of his late valued friend Dr. John Reid, in the "Edinb. Med. and Surg. Journal" for April, 1841; and Dr. Reid's "Physiological, Pathological, and Anatomical Researches," CHAP. II.

nutrient actions to which it was subservient; it being found, by examination of the limb after its removal, that both the larger tubes and the capillaries were pervious throughout, so that no mechanical impediment existed, to prevent the propulsive power of the heart from transmitting the blood through them. The influence of the prolonged application of cold to a part, may be referred-to in support of the same general proposition; for although the calibre of the vessels is diminished by this agent, yet their contraction is not sufficient to account for that complete cessation of the flow of blood through them, which precedes the entire loss of their vitality.—A periodical retardation or suspension of the circulation in particular portions of the body, unaccompanied by any other ostensible change, and not dependent upon any failure of the heart's power, is by no means an uncommon phenomenon. It frequently presents itself, for example, in one of the fingers; and a curious case is recorded by Dr. Graves,* in which the whole of one leg was thus affected, with remarkable periodicity, for about twelve hours out of the twenty-four; whilst in the intervals the circulation in the limb was unusually active, the action of the heart being quite natural throughout, and the circulation in the rest of the body not being in the least affected.

250. In the development of the embryo of the higher Vertebrated animals, moreover, there is a period at which a distinct movement of red blood is seen, before any pulsating vessel can be detected to possess an influence over it (§ 255). Further, instances not very unfrequently occur, of fœtuses having attained nearly their full development, which have been unpossessed of a heart, and in which the circulation has been, as it were, entirely capillary; and although in most, if not all, of these cases, the monster has been accompanied by a perfect child, the heart of which may have been suspected to have influenced its own circulation, yet, in one of those most recently examined, the occurrence of this has been disproved. From a careful examination of the vascular system, it appeared impossible that the heart of the twin fœtus could have caused the movement of blood in the imperfect one; and this must, therefore, have been maintained by forces arising out of the nutritive changes occurring in the capillaries.†

251. All these circumstances indicate that the movement of blood through the Capillaries is very much *influenced* by local forces; although these forces are not sufficiently powerful, in the fully-developed state of the higher animals, to *maintain* it by themselves. And from other facts it appears, that the conditions necessary for the energetic flow of blood through these vessels, are nothing else than the active performance of the nutritive and other operations, to which its movement is subservient. —The principle already noticed (§ 205) as having been developed by Prof. Draper, seems fully adequate to explain these phenomena. It will

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* "Lectures on Clinical Medicine," second edition, Vol. i., p. 73.

† For the details of this interesting case, which was communicated by Dr. Houston of Dublin to the British Association in 1836, see the "British and Foreign Medical Review," Vol. ii. p. 596, and the "Dublin Medical Journal" for 1837. An attempt was made by Dr. Marshall Hall ("Edinb. Monthly Journal," 1843) to disprove Dr. Houston's inferences; but a most satisfactory reply was made by Dr. H. in the "Dublin Journal" for Jan. 1844. See also the "Edinb. Med. and Surg. Journal," July, 1844.—A similar case is recorded by Dr. Jackson, of Boston (N.E.) in the "American Journal of the Medical Sciences," Feb. 1838.

be convenient to take the Respiratory circulation as an example of its application; since the changes to which this is subservient, are more simple than those which take place elsewhere. The venous blood transmitted to the lungs, and the oxygen in the pulmonary cells, have a mutual attraction, which is satisfied by the exchange of oxygen and carbonic acid that takes place through the walls of the capillaries; but when the blood has become arterialised, it no longer has any such attraction for the air. The venous blood, therefore, will drive the arterial before it, in the pulmonary capillaries, whilst respiration is properly going on: but if the supply of oxygen be interrupted, so that the blood is no longer aerated, no change in the affinities takes place whilst it traverses the capillary network; the blood, continuing venous, still retains its need of a change and its attraction for the walls of the capillaries; and its egress into the pulmonary veins is thus resisted, rather than aided, by the force generated in the lungs.—In the Systemic circulation, the changes are of a much more complex nature, every distinct organ attracting to itself the peculiar substances which it requires as the materials of its own nutrition; and the nature of the affinities thus generated will be consequently different in each case. But the same principle holds good in all instances. Thus, the blood conveyed to the liver by the portal vein, contains the materials at the expense of which the bile-secreting cells are developed; consequently the tissue of the liver, which is principally made-up of these cells, possesses a certain degree of affinity or attraction for blood containing such materials; and this is diminished, so soon as they have been drawn from it into the cells around. Consequently the blood of the portal vein will drive before it, into the hepatic vein, the blood which has already traversed the capillaries of the portal system, and which has given-up, in doing so, the elements of bile to the solid tissues of the liver.

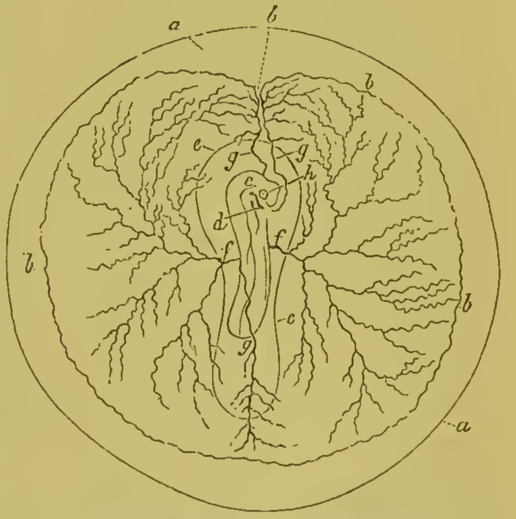
252. We are now prepared, therefore, to understand the general principle, that the rapidity of the local circulation of a part will depend in great measure upon the activity of the functional changes taking place in that part,—the heart's action, and the state of the *general* circulation, remaining the same. When, by the heightened vitality, or the unusual exercise, of any organ, the changes which the blood naturally undergoes in it are increased in amount, the affinities which draw the arterial blood into the capillaries are stronger, and are more speedily satisfied, and the venous blood is therefore driven out with increased energy. Thus a larger quantity of blood will pass through the capillaries of the part in a given time, without any enlargement of their calibre, or even though it be somewhat diminished; but the size of the arteries by which it is conveyed soon undergoes an increase, adapting them to supply the increased demand. Any circumstance, then, which increases the functional energy of a part, or stimulates it to increased nutrition, will occasion an increase in the supply of blood, altogether irrespectively of any change in the heart's action. This principle has long been known, and has been expressed in the concise adage "*Ubi stimulus, ibi fluxus;*" which those Physiologists, who affirm that the Circulation is maintained and governed by the heart alone, cast into unmerited neglect.

253. The development of that Circulating system which has been described as peculiar to the higher classes of Vertebrated animals, is not

completed until the moment of birth; and the progressive changes which the heart and vascular apparatus undergo, in the evolution of the fœtus of Birds and Mammals, afford a most beautiful illustration of the principles already laid down (§ 74), respecting the amount of correspondence between the transitory stages of each system in the higher animals, and the forms permanently exhibited by the lower. It has been seen that in the organs of Circulation, as well as in all others, the tendency, as we rise from their lowest to their highest condition, is one of specialization. In the simplest Animals, as in Plants, whatever motion of fluid takes place is effected in each individual part *by* and *for* itself; whilst in the complex and highly-developed structures that occupy the other extremity of the scale, the evolution of a powerful organ of impulsion, the influence of which extends over the whole system, has superseded the diffused agency by which the circulation was previously maintained. This progress from a more general to a more special type is equally manifested in the vascular system of the embryo; and the analogy which thus arises between the forms it presents at different epochs of its development, and those presented by the lower tribes of animals, is not superficial only, but extends even to minute particulars. The egg of the Bird affords the best opportunity for studying the early changes which it undergoes, and these have been determined with great minuteness; but such a sketch of them only can here be given, as will serve to illustrate the principles alluded to. The preliminary stages of the process will be described in their proper place (CHAP. XI).

254. At an early period of incubation, the yolk is found to be enveloped by a 'germinal membrane,' composed of distinct cells, which is divisible into three layers; and a thickened portion of this is easily distinguishable, at which the embryo will be subsequently evolved. The middle layer gives origin to the Circulating system, and is therefore termed the *vascular* layer. The thickened portion of this, that surrounds the germ, soon becomes studded with numerous irregular points and marks of a dark yellow colour; and as incubation proceeds, these points become more apparent, and are gradually elongated into small lines, which are united together, first in small groups, and then into one network, so as to form what is called the *Vascular area* (Fig. 133). A large dark spot of a similar kind is seen in the situation to be subsequently occupied by the heart. These dark points and lines are formed by collections of blood-corpuscles, which originate in the transformation of the cells of the embryo and of the germinal membrane; and the rows and masses of blood-disks seem at

FIG. 133.



Vascular Area of *Fowl's* egg, at the beginning of the third day of incubation;—*a*, *a*, yolk; *b*, *b*, *b*, *b*, venous sinus bounding the area; *c*, aorta; *d*, punctum saliens, or incipient heart; *e*, *e*, area pellucida; *f*, *f*, arteries of the vascular area; *g*, *g*, veins; *h*, eye.

first to lie in mere channels, the walls of the heart and blood-vessels that subsequently enclose them, being of later formation. From the first, however, a definite plan is perceptible; the network of capillaries that is formed over the vascular area, being supplied with blood by the ramifications of a pair of arterial trunks *f*, *f*; whilst the blood is collected from them by the circular venous sinus *b*, *b*, which bounds the area, and is returned to the embryo by the venous trunks *g*, *g*. In the blood-vessels which are first observed in the body of the embryo, as well as in the vascular area, no difference is perceptible between the characters of the arteries and those of the veins; and these are only to be distinguished by the direction of the currents of blood circulating through them. But at about the fourth or fifth day of incubation, the coats of the arteries begin to appear thicker than those of the veins, and the distinction between them soon becomes evident. After the principal vessels are formed, the development of new ones seems to take place in two modes, according as they are to occupy the interspaces existing among those previously formed, or are to extend themselves into out-growing parts. In the first of these cases, the new capillaries appear to be formed, like the original ones, from stellate cells, whose prolongations meet the vessels in which blood is already circulating, coalesce with them, and thus receive the current into their own cavities, to transmit it to some other vessel; but in the second, the new vessels are formed entirely by outgrowth from those already existing (§ 211).

255. The first rudiment of the Heart appears about the 27th hour, and is a mass of cells, of which the innermost soon break down, so as to form a tubular cavity; for some time it is simple and undivided, extending, however, through nearly the whole length of the embryo; but the posterior part may be regarded as corresponding with the future auricle, since prolongations may be perceived to stretch from that part into the transparent area, which indicate the place where the veins subsequently enter. Although the development has proceeded thus far at about the 35th hour, no motion of fluid is seen in the heart or vessels until the 38th or 40th hour. When the heart first begins to pulsate, it contains only colourless fluid mixed with a few globules. A movement of the dark blood in the circumference of the vascular area is at the same time perceived; but this is independent of the contractions of the heart; and it is not until a subsequent period, that such a communication is established between the heart and the distant vessels, that the dark fluid contained in them arrives at the central cavity, and is propelled by its pulsations. This fact, which we have just seen to possess a very important bearing on the theory of the circulation, and which has been denied by some observers, appears to have been positively established by the researches of Von Baer.*—The contraction of this dorsal vessel (for so it

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* He says that there is no doubt of the blood being formed before the vessels. The formation of the blood goes on in every part of the body; and when formed, it is put in motion by some unknown cause that impels it in the proper direction, until at length it reaches the central formation of blood, around which is developed a tubular canal afterwards to be further modified and changed into a heart. The first motions of the blood are *towards* the heart, and consequently the first vessels formed are *veins;* a fact of itself sufficient to disprove the hypothesis that the motive power which presides over the circulation resides exclusively in the ventricles of the heart.—"Uber Entwickelungsgeschicte der Thiere," &c. Part II. p. 126.

might be termed) begins at its posterior extremity, and gradually extends itself to the anterior; but, between the 40th and 50th hours, a separation in its parts may be observed, which is effected by a constriction round the middle of the tube; and the dilatation of the posterior portion becomes an auricular sac, and that of the anterior a ventricular cavity. Between the 50th and 60th hours, the circulation of the blood in the vascular area becomes more vigorous, and the action of the ventricle is no longer continuous with that of the auricle, but seems to succeed it at a separate period. At the same time the tube of the heart becomes more and more bent together, until it is doubled; so that this organ now becomes much shorter relatively to the dimensions of the body, and is more confined to the portion of the trunk to which it is subsequently restricted. The convex side of the curve which the tube presents, is that which subsequently becomes the apex or point of the heart; and, between the 60th and 70th hours, this is seen to project forward from the breast of the embryo, much in the situation it subsequently occupies. About the same time, the texture of the ventricle differentiates itself considerably from that of the auricle; the auricle retaining the thin and membranous walls which it at first possessed, while the ventricle becomes stronger and thicker, both its internal and external surfaces being marked by the interlacement of muscular fibres, as in the higher Mollusca. About the 65th hour, the grade of development of the heart may be regarded as corresponding with that of the Fish, the auricle and ventricle being perfectly distinct; but their cavities are as yet quite single.—The heart of the Dog at the 21st day bears a great resemblance to that of the Chick at the 55th or 60th hour; it consists of a membranous tube twisted on itself, and partially divided into two principal cavities, besides the bulb or dilatation which at this period is found at the commencement of the aorta, and which corresponds with the bulbus arteriosus of Fishes.

Fig. 134.

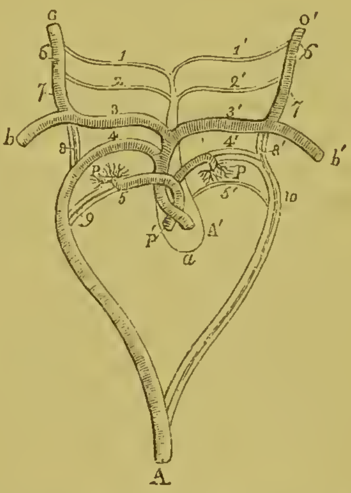

Diagram of the formation of the great Arterial trunks in the *Chick*:—A, descending aorta; A′, ascending aorta; P, P, pulmonary arteries; P′, their common trunk; *a*, truncus arteriosus; *b*, *b*′, subclavian arteries; *c*, *c*′, carotid arteries; 1, 1′, 2, 2′, 3, 3′, 4, 4′, 5, 5′, five pairs of branchial arches; 6, 6′, 7, 7′, communicating branches which become the trunks of the carotids; 8, 8′, communicating branches afterwards obliterated; 9, ductus arteriosus; 10, aortic arch of the left side.

256. Having thus traced the evolution of the heart of the Chick up to the grade which it presents in Fishes, we may now enquire what is the condition of the other parts of the vascular system at the same time. At the end of the second day, the primitive arterial trunk or 'bulbus arteriosus,' (Fig. 134, *a*) is seen to have given off two canals, 1, 1′, which separate from one another to enclose the pharynx, and then unite again to form the aortic trunk, A, which passes down the spine. During the first half of the third day (about the 60th hour), a second pair of arches, 2, 2′, is formed, which encompasses the pharynx in the same manner; and towards the end of the

third day, two other pairs of vascular arches, 3, 3′, and 4, 4′, are formed; so that the pharynx is now encompassed by four pairs of vessels, which unite again to supply the general circulation. These evidently correspond with the branchial arches of Fishes, although no respiratory apparatus is connected with them; and in fact the distribution of the vascular system of the Bird, on the fourth and fifth days, exactly resembles that presented by many Cartilaginous Fishes, as well as by the larvæ of the Batrachia. The first pair of arches is obliterated about the end of the fourth day; but a pair of vessels, which are sent from it to the head and neighbouring parts, and which afterwards remain as the carotid arteries, *c*, *c*′, continue to be supplied through communicating vessels, 6, 6′, from the second arch. While the first pair is being obliterated, a fifth, 5, 5′, is formed behind the four which had previously existed; and proceeds, in the same manner as the fourth, from the ascending to the descending aorta. On the fourth day, the second arch also becomes less, and on the fifth day it is wholly obliterated; whilst the third and fourth become stronger. From the third arch, now the most anterior of those remaining, the arteries are given off which supply the upper extremities, *b*, *b*′; and the vessels of the head, *c*, *c*′, are now brought into connection with it, by means of the communicating branches, 7, 7′, which previously joined the third with the second arch. When these vessels are fully developed, the branches, 8, 8′, by which these arches formerly sent their blood into the aorta, shrink and gradually disappear; so that, by about the thirteenth or fourteenth day, the whole of the blood sent through the two anterior arches (the second and third) is carried to the head and upper extremities, instead of being transmitted to the descending aorta as before. There now only remain the fourth and fifth pairs of branchial arches; the development of which into the aorta and pulmonary arteries, will be described in connection with the changes that are at the same time going-on in the heart.

257. During the fourth day, the cavities of the Heart begin to be divided, for the separation of the right and left auricles and ventricles. About the 80th hour, the commencement of the division of the auricle is indicated externally, by the appearance of a dark line on the upper part of its wall; and this, after a few hours, is perceived to be due to a contraction, which, increasing downwards across the cavity, divides it into two nearly spherical sacs. Of these the right is at first much the larger, and receives the great systemic veins, whilst the left has the aspect of a mere appendage to the right; but it subsequently receives the veins from the lungs, when these organs are developed, and attains an increased size. The septum between the auricles is by no means completed at once; a large aperture (which subsequently becomes the *foramen ovale*) exists for some time at its lower part, so that the ventricle continues to communicate freely with both auricles. This passage is afterwards closed by the prolongation of a valvular fold, which meets it in the opposite direction; it remains pervious, however, until the animal begins to respire by the lungs, and sometimes is not completely obliterated even then. The division of the ventricle commences *some time before* that of the auricle, and is effected by a sort of duplicature of its wall, forming a fissure on its exterior and a projection within; and thus a septum is gradually developed within the cavity, which progressively acquires

firmness, and rises higher up, until it reaches the entrance to the bulb of the aorta, where some communication exists for a day or two longer. At last, however, the division is completed, and the inter-ventricular septum becomes continuous with the inter-auricular, so that the heart may be henceforth regarded as a double organ. The progressive stages presented in the development of this septum, are evidently analogous to its permanent conditions in the various species of Reptiles (§ 244); but it must not be lost sight of, that in all Reptiles the inter-auricular septum is first developed, and that it is completely formed in many instances in which the inter-ventricular septum is absent or imperfect.—The changes which occur in the heart of the Mammalia, are of a precisely similar character; and as they take place more slowly, they may be watched with greater precision. Soon after the septum of the ventricles begins to be formed in the interior, a corresponding notch appears on the exterior, which, as it gradually deepens, renders the apex of the heart double. This notch between the right and left ventricles continues to become deeper, until about the eighth week in the Human embryo, when the two ventricles are quite separated from one another, except at their bases; this fact is very interesting, from its relation with the similar permanent form presented by the heart of the Dugong (§ 245). At this period, the internal septum is still imperfect, so that the ventricular cavities communicate with each other, as in the chick, on the fourth day. After the eighth week, however, the septum is complete, so that the cavities are entirely insulated; whilst at the same time their external walls become more connected towards their bases, and the notch between them is diminished; and at the end of the third month the ventricles are very little separated from one another, though the place where the notch previously existed is still strongly marked.

258. Returning again to the distribution of the Arterial trunks, we are now prepared to follow their final modification, by which they are adapted to the existence which the individual is soon to commence as an air-breathing animal.—The first, second, and third (branchial) arches have been shown to be replaced by the brachial and carotid arteries, and to have lost all communication with the primitive arterial trunk (Fig. 134, *a*) except at its commencement, where the third pair of arches arises with the other trunks from its dilated bulb. This remains as a single cavity, even after the ventricles have been separated; but towards the end of the fifth or beginning of the sixth day, in the Chick, the bulb becomes flattened, and the opposite sides adhere together, so as to divide it into two tubes running side by side. Of these, one communicates with the left, and the other with the right ventricle. The former, which subsequently becomes the ascending aorta, A′, is continuous with the fourth branchial arch, 4, on the right side only; but from this the carotid and brachial arteries arise by two principal trunks. This arch becomes gradually larger, so as to form the freest mode of communication between the heart and the descending aorta; it subsequently becomes, in fact, the arch of the aorta. The trunk P′, which is connected with the right ventricle, on the other hand, and which subsequently becomes the pulmonary artery, transmits its blood through the fourth arch of the left side, 4′, and the fifth arch, 5, of the right (the two primary tubes twisting round each other); but the fifth arch on the left side, 5′, now ceases

to convey blood. From the two trunks, 4′, 5, which still discharge their blood into the descending aorta, the pulmonary vessels, P, P, branch off as the lungs are developed; and the prolongation, 10, of the former of these, which previously constituted one of the arches of the descending aorta, soon afterwards becomes impervious. The original prolongation, 9, of the latter trunk, which meets the descending aorta, still remains; so that a portion of the blood sent from the right ventricle is transmitted through this communicating branch directly into the descending aorta, just as in the adult Crocodile. After the first inspiration, however, the whole of the blood transmitted through the pulmonary artery passes into the lungs, and does not enter the aorta until it has been returned to the heart; and this communicating vessel, which is termed the *ductus arteriosus*, soon shrinks and becomes impervious. Thus the *third* pair of branchial arches becomes converted into the two *arteriæ innominatæ*, or common trunks, from each of which, in Birds and in some Mammals, the carotid and subclavian arteries of one side originate. The *fourth* branchial arch of the *right* side becomes the *arch of the aorta*. And the *fifth* branchial arch of the *right* side, with the *fourth* of the *left*, become the right and left pulmonary arteries.—The general plan of the changes which occur in the vascular system of the Mammalia (Fig. 135), is the same as that which has been described in Birds, the differences being only in detail; as for instance, that the aortic arch is formed, not from the right, but from the left branchial arch.

259. Up to the period of the hatching of the egg in Birds, and the separation of the fœtus from the parent in the Mammalia, the circulation retains some peculiarities, characteristic of the inferior type which is permanent in the Reptile tribes. Of the blood which is brought by the venous trunks to the right auricle, part has been purified by transmission to the respiratory organ (the *allantois* in Birds, and the *placenta* in Mammals), whilst a part has been vitiated by circulation through the system. The former, returning by the umbilical vein (Fig. 135, *o*), is mixed in the ascending vena cava (*j*) with the blood which has circulated through the lower extremities; whilst the descending cava brings back that which has passed through the capillaries of the head and upper extremities, and which, having received no admixture of arterial blood, is not fit to be again transmitted in the same condition. It will be recollected that a communication still exists between the two auricles, the 'foramen ovale' yet remaining pervious; and by a fold of the lining membrane of the right auricle, forming the Eustachian valve, the ascending and descending currents are so directed, that the former (consisting of the most highly-arterialised blood) passes at once into the left auricle, whilst the latter flows into the right ventricle.* From the left auricle, the arterial blood is propelled into the left ventricle, and thence through the arch of the aorta to the vessels of the head and upper extremities, a comparatively small part finding its way into the descending aorta. The venous current is propelled through the pulmonary artery; but the lungs not yet being expanded, little of it is transmitted to these organs, and

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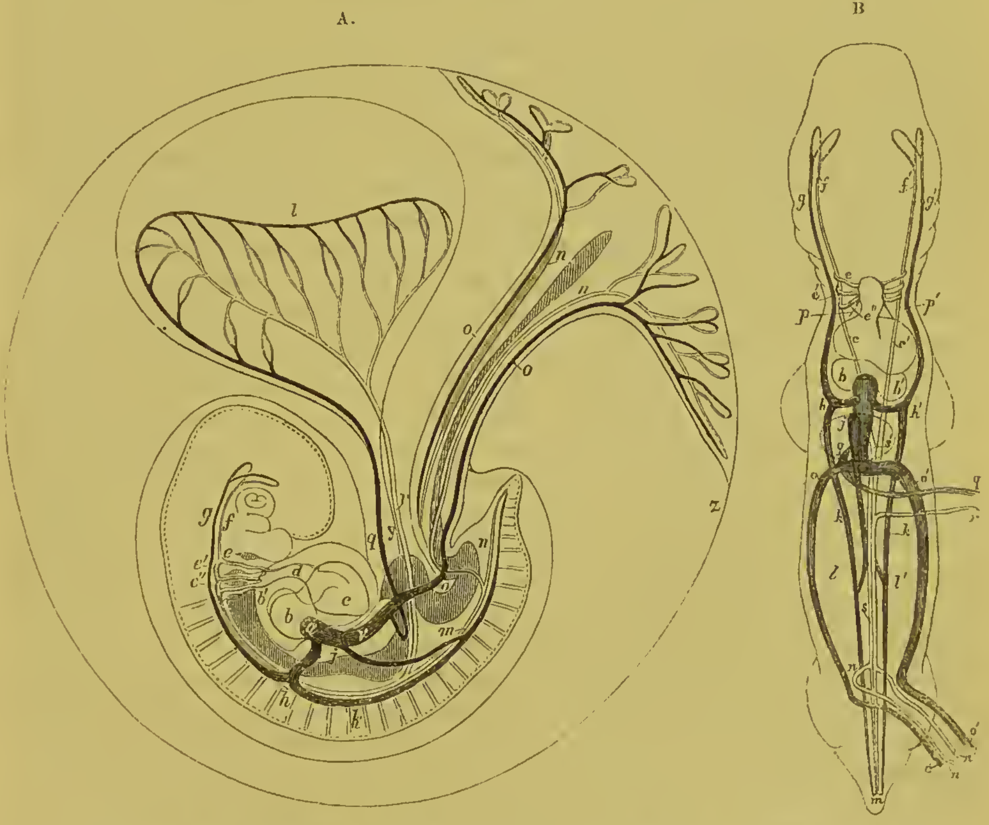
* The peculiar course taken by the blood through the heart, which was suspected from anatomical investigation, has been actually demonstrated by means of coloured injections, by Dr. J. Reid. See "Edinb. Med. and Surg. Journ.," Vol. xliii., pp. 11 and 308; and Dr. Reid's "Physiol., Pathol., and Anat. Researches," Chap. ix.

the greater part finds its way through the ductus arteriosus into the descending aorta, where it mixes with the remainder of the first-mentioned portion. This trunk not only supplies the viscera and lower extremities (which are thus seen to receive, as in Reptiles, blood of which only a portion has been oxygenated), but sends a large proportion of its contents to the umbilical vessels, by which it is conveyed to the oxygenating organ, and returned again to the venous trunk of the abdomen.

260. The course of development of the Venous system exhibits not less remarkably than that of the Arterial, a gradual passage from the more general type common to all Vertebrata at an early period of their existence, and perpetuated with but little alteration in Fishes, to that more special type which presents itself in the complete Bird or Mammal. —There is at first a pair of anterior venous trunks (Fig. 135, A, B, *g*, *g′*) receiving the blood from the head, and a pair of posterior trunks (*k*, *k′*) formed by the confluence of the veins of the trunk, Wolffian bodies, &c.; the former are persistent as the 'jugular' veins; the latter remain separate

FIG. 135.



A.—Diagram of the Circulation in the *Human Embryo* and its appendages, as seen in profile from the right side, at the commencement of the formation of the Placenta:—B. The same, as seen from the front:—*a*, venous sinus, receiving all the systemic veins; *b*, right auricle; *b′*, left auricle; *c*, right ventricle; *c′*, left ventricle; *d*, bulbus aorticus, subdividing into *e*, *e′*, *e″*, branchial arteries; *f*, *f′*, arterial trunks, formed by their confluence; *g*, *g′*, vena azygos superior; *h*, *h′*, confluence of the superior and inferior azygos; *j*, vena cava inferior; *k*, *k′*, vena azygos inferior; *l*, *l′*, anastomosis of inferior cava with inferior azygos veins; *m*, descending aorta; *n*, *n′*, umbilical arteries proceeding from it; *o*, *o′*, umbilical veins, of which the right afterwards disappears, the left being alone fully developed; *q*, omphalo-mesenteric vein; *r*, omphalo-mesenteric artery, distributed on the walls of the vitelline vesicle *t*; *v*, ductus venosus; *y*, vitelline duct; *z*, chorion.

in most Fishes, where they are designated the 'cardinal' veins; but in warm-blooded Vertebrata, they are only represented by the 'azygos' veins (major and minor), which coalesce into a common trunk for a considerable part of their length. One of the anterior trunks unites with one of the posterior on either side, to form a canal which is known as the 'ductus Cuvieri;' and the ducts of the two sides coalesce to form a shorter main canal, which enters the auricle, at that time an undivided cavity. This common canal is absorbed (so to speak) into the auricle, at an early period, in all Vertebrata above Fishes, so that the two Cuvierian ducts terminate separately in that cavity; and after the septum auriculorum has been formed, they enter the right auricle.—This arrangement is persistent in Birds and in the inferior Mammals, in which we find two 'venæ cavæ superiores,' entering the right auricle separately; but in the higher Mammals, as in Man, the left duct is obliterated, and the right alone remains to form the single vena cava superior, a transverse branch being formed to bring to it the blood of the left side. The double vena cava sometimes remains persistent in Man, constituting a monstrosity by arrest of development. As the anterior extremities are developed, the subclavian veins are formed to return the blood from them; and these discharge themselves into the jugular.—The 'omphalo-mesenteric' vein (*q*), which is another primitive trunk common to all Vertebrata, is formed by the confluence of the veins of the yolk-bag and of the intestinal canal, and passes by itself, with the two Cuvierian ducts, into the auricle. The upper part of this remains to constitute the upper part of the 'inferior cava,' the lower portion of which arises between the Wolffian bodies, and originally enters the omphalo-mesenteric vein above the liver. When the liver is formed, the omphalo-mesenteric vein becomes connected with it both by afferent and efferent trunks, the former remaining as the 'vena portæ,' and the latter as the 'hepatic vein;' and after giving off the former trunks, the omphalo-mesenteric vein is itself obliterated, so that all the blood which it brings must pass through the liver. The 'inferior cava,' which receives the hepatic vein, is gradually enlarged by the reception of most of the veins from the inferior part of the trunk and the lower extremities, and the vena azygos is reduced in the same proportion; in some rare cases of abnornal formation, however, the vena cava fails to be developed, and then the blood from the lower parts of the body is conveyed to the superior cava through the azygous system.*—The umbilical vein, which is at first developed in connection with the allantois, and which consequently does not exist where that organ is not evolved, increases in size as the mesenteric artery diminishes; the greater part of its blood is discharged into the vena portæ, and only reaches the inferior cava after passing through the liver; but a part of it passes-on to the vena cava through a direct channel, which constitutes the 'ductus venosus.' A similar direct communication between the portal system and the vena cava exists permanently in Fishes, and to a less degree in other oviparous Vertebrata: and it seems there intended to transmit directly to the heart whatever proportion of the blood, brought to the vena portæ, may be at the time superfluous as regards the function of the liver. After the birth of the Mammal, however, its portal system receives no more blood than is required for distribution through the liver; and the ductus venosus speedily shrivels into a ligament.

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* For the details of the changes above described, see Rathke "Ueber den Bau und die Entwickelung des venen systems der Wirbelthiere," 1838; and Mr. Marshall's Memoir 'On the Development of the Great Anterior Veins in Man and Mammalia,' in "Philos. Transact.," 1850.

261. Thus we have traced, in the development of the Circulating apparatus of the higher Vertebrata, the same progressive advance from a more *general* to a more *special* condition, as that which we have witnessed in ascending the Animal series; and when considered *analogically* rather than *homologically* (§ 8), the correspondence is extremely close. For in the state of the circulating system in the early embryo, when the heart is as yet but a pulsating enlargement of one of the principal trunks, and the walls of the vessels are far from being complete, we have the representation of its condition in the higher Radiata, and in the lower Articulata and Mollusca. In the subsequent division of the cardiac cavity into an auricle and a ventricle, an advance is made corresponding to that which we encounter in passing from the Tunicata to the higher Mollusca. And when the branchial arches are formed, which enclose the pharynx and meet in the aorta, the type of the Fish is obviously attained.—But it will be observed that, notwithstanding this similarity, the Vertebrated embryo never presents any of those features of the Circulating apparatus, which are characteristic of the other sub-kingdoms respectively; thus, it does not exhibit that radiated distribution of the vascular trunks, which is seen in the *Echinodermata* (§ 216); nor does the heart, even when most like a 'dorsal vessel,' ever present the least approach to that transverse division into successive segments, which is typical of the *Articulata* (§ 217); and in its position and connections, being situated in the immediate neighbourhood of the pharynx, and sending its primitive trunks around it, the heart of every Vertebrated animal differs from that of the *Mollusca*, whose relations are with the opposite extremity of the alimentary canal (§ 234). In the subsequent progress of the Circulating apparatus, from the grade of the Fish, through that of the Reptile, to that of the Bird or Mammal, we have a characteristic illustration of the principles formerly laid down (§ 74); for although the branchial arches are formed in *all* Vertebrated animals, yet it is only in Fishes and Batrachian Reptiles that they give origin to branchial tufts; and although at a subsequent period the condition of the heart and great vessels presents a strong general resemblance to that of the typical Reptiles, yet that resemblance is wanting in the essential feature of the complete separation of the auricles, and the mixture of arterial and venous blood in the single ventricle. It is obvious that this want of conformity has reference to the difference in the seat of the respiratory process; the pulmonary vessels in the embryo being developed for future use, but the actual aeration of the blood being performed elsewhere.

262. The knowledge of these different stages of the development of the Circulating apparatus, enables us to explain many of the malformations which are occasionally presented in Man. One of the most common of them gives rise to the malady termed *Cyanosis;* for this results from the *foramen ovale*, which establishes a communication between the auricles, remaining open after pulmonary respiration has been established; so that a considerable portion of the blood transmitted to the right cavity passes

into the left, without having been previously arterialised by passage through the lungs. Persons thus affected have always a livid aspect; from the quantity of venous blood circulated through the arteries; they are deficient in muscular energy and in power of generating heat, and they are seldom long-lived. A consequence partly similar would probably have resulted from a curious malformation mentioned by Kilian, had the infant remained alive: in this case, the aortic arch had not been developed, so that the primary aortic trunk gave off only the vessels to the head and upper extremities: whilst the communicating branch between the pulmonary artery and descending aorta, which usually is of a secondary character, constituting the ductus arteriosus, was here the only means by which the blood could be transmitted to the latter; so that the circulation through the lower part of the trunk and extremities would have been entirely venous. A malformation of this kind in a diminished degree has not been found incompatible with the continuance of life; several cases being on record, in which the ductus arteriosus has remained pervious, and has brought part of the blood from the pulmonary artery to the descending aorta. Cyanosis is of course, as in the former instance, the result of this imperfect arterialisation; and the individual is reduced, as far as his vascular system is concerned, to the condition of the Crocodile. An arrest of development at an earlier period may cause still greater imperfections in the formation of the heart. Thus, the septum of the ventricles is sometimes found incomplete, the communication between the cavities usually occurring in the part which is last formed, and which in most Reptiles remains open. In other cases it has been altogether wanting, although the aorta and pulmonary artery were both present, and arose side by side from the common cavity; and this form of the circulating apparatus is evidently analogous to that presented by Reptiles in general. A still greater degradation in its character has been occasionally evinced; for several cases are now on record, in which the heart has presented but two cavities, an auricle and a ventricle, thus corresponding with that of the Fish; and in one of these instances the child had lived for seven days, and its functions had been apparently but little disturbed. The occasional entire absence of the heart has already been noticed; and coexistent with this, there is always great deficiency in the other organs; the brain, and sometimes the liver and stomach, being undeveloped. The bifid character of the apex, which presents itself at an early period of the development of the heart, and is permanent in the Dugong, sometimes occurs as a malformation in the adult human subject; evidently resulting, like the others which have been mentioned, from an arrest of development. On similar principles, some occasional peculiarities noticed in the distribution of the vessels may be accounted-for, of which a striking example will be presently given. The ascending Cava is occasionally observed to consist of two parallel trunks, which are partially united at intervals, and then separate again; a similar condition is permanent in some Cartilaginous Fishes, and the explanation of it is to be sought-for in the history of the development of the venous system in general. We have seen that in many of the lower animals, such as the Crustacea, where the arteries are perfect canals, having distinct coats, the veins seem to be merely channels through the tissues, having no definite walls: in like manner, at an early period of the fœtal development of the higher animals, several small vessels are found where one vein subsequently exists; and, if the coalescence of these has been from any cause checked, they will remain permanently separated to a greater or less extent.

263. Several interesting varieties have been detected in the arrangement of the principal trunks given-off from the Aorta: and though we cannot account for them on the principles already mentioned, it is not a little curious, that nearly all of these irregular forms possess analogues in the arrangements which are peculiar to some or other of the Mammalia. The mode in which the cephalic and brachial vessels usually arise in the Human subject, is shown in the subjoined diagram, A, where *a b* is the arch of the aorta, 1 and 2 the trunks of the right carotid (which supplies the head) and of the right subclavian (which is distributed to the upper extremity), arising by a common trunk—the arteria innominata; while the left carotid, 3, and the left subclavian, 4, arise separately. At B is seen a distribution which is rare in the human subject, the two carotids arising by a common trunk, and the right as well as the left subclavian being given off separately; this is the regular arrangement of branches in the Elephant. It is not so unusual for all the branches to arise from single trunks as at C; and this appears to be the regular type in some of the Cetacea. Sometimes, again, there is an arteria innominata on each side; subsequently dividing into the carotid and subclavian, as at D; and on this plan the branches are distributed in the Bat tribe, and also in the Porpoise. A not unfrequent variety in the human subject, is for both carotids to arise with the right subclavian from a single trunk, as at E, the left subclavian coming off by itself; this is observable as the regular form among many animals, being common among the Monkey tribe, the Carnivora, the Rodentia, &c. Another variety which is not unfrequent is shown at F, the vertebral artery on the left side, 5, which usually arises from the subclavian, springing directly from the aorta; it is on this plan that the branches are given off in the Seal. A form which is very uncommon in man is that represented at G; here the aorta divides at once into an ascending vessel, from which the two subclavian and two carotid arteries arise, and a descending trunk; this is the regular distribution of the vessels in Ruminating animals, and appears to be most general in Mammalia possessing a long neck. Lastly, at H, is seen a form which evidently results from an arrest of the usual changes in the arterial trunks described in §§ 256, 258; the aorta continuing to

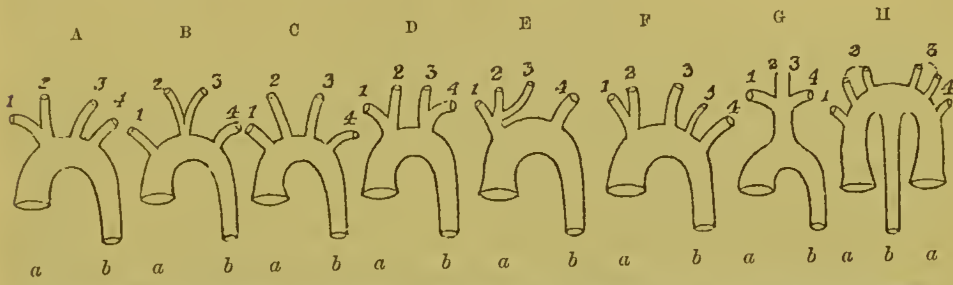

Diagram of the principal varieties in the origin of the Cephalic and Brachial trunks from the arch of the Aorta;—A, Man; B, Elephant; C, Cetacea; D, Bat, &c.; E, Carnivora, &c.; F, Seal; G, Ruminants; H, Reptiles:—1, right subclavian; 2, right carotid; 3, left carotid; 4, left subclavian; 5, vertebral; *a*, ascending aorta; *b*, descending aorta.

possess a double arch, from the ascending part of which the subclavian, external carotid, and internal carotid arteries are given-off on each side, the single descending trunk being formed by the union of the two original branches. This, it will be recollected, is the normal type of formation in Reptiles.*

CHAPTER VI.

OF RESPIRATION.

1. *General Considerations.*

264. THE function of Respiration essentially consists in the *evolution of carbonic acid* from the fluids of Organised beings, and the *absorption of oxygen* from the surrounding medium, usually in a nearly equivalent proportion. This process is performed by Plants as well as by Animals; and it may be regarded as arising out of the same *general* requirements in both kingdoms, although it answers some *special* purposes in the latter, which render it more immediately essential to the maintenance of their vital activity, than it seems to be in the former. For we shall hereafter find that the imperious necessity for the continual introduction of oxygen and liberation of carbonic acid, which requires a most active performance of the respiratory function, and causes even a brief suspension of it to be fatal, in the higher Animals, is consequent upon the energetic exertion of their peculiarly *animal* powers, and upon the performance of that combustive operation by which their high temperature is maintained; whilst, on the other hand, when we pass to those tribes which are most remarkable for the inertness of their habits, and for their entire want of power to sustain an independent temperature, the demand for oxygen is greatly diminished, and the exhalation of carbonic acid may be checked for a time without injury. The amount of Respiration, then, which is required for the performance of the *organic* or constructive functions of Animals, is comparatively small; and it is not surprising that the existence of this function should have been long overlooked in Plants, in which its effects on the atmosphere are masked by a change of an entirely opposite nature, that is subservient to the introduction of alimentary material into the system,—namely, the decomposition of the carbonic acid of the air, under the influence of light, the fixation of its carbon in the vegetable tissues, and the consequent liberation of its oxygen. To this last process, the term Respiration has been commonly applied; and the Respiration of Plants is ordinarily spoken-of as antagonistic to that of Animals. This statement is perfectly true, if under the term Respiration be included the sum-total of the changes produced in the air by the growth of a Plant; but it will be presently shown, that whilst Animal life gives

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* In the foregoing account of the development of the Vascular system, the Author has availed himself freely of the valuable papers of Dr. Allen Thomson, in the "Edinb. Philos. Journal," Vols. ix. and x.; in the sketch of the malformations of the Heart, he has made use of the paper of Dr. Paget in the "Edinb. Med. and Surg. Journal," Vol. xxxvi.; and the last paragraph, with the accompanying figures, has been entirely derived from the magnificent work of Tiedemann on the "Anatomy of the Arteries."

rise to but one set of changes in the atmosphere (namely, the removal of a portion of its oxygen, and a replacement of this by carbonic acid), Vegetable life produces two sets of changes, which ought to be kept quite distinct from each other in a scientific description of them, their nature and their sources being alike different; and that it is only on account of the excess of one set of these changes beyond that which it antagonises, that *it* alone has received general attention, and has been commonly regarded as the proper respiration of Plants.

265. Restricting the meaning of the term *Respiration*, then, to the removal of carbonic acid from the living system in a gaseous form, and the introduction of oxygen into it, we have to enquire what are those most general sources of demand for this action in the vital economy, which are common to Plants and Animals. These appear to be two-fold; one arising out of the *disintegrating* changes which are always going-on in the living system; the other being consequent upon some of those chemical operations, which necessarily participate in the *constructive* functions. The former seem to be the most general; the latter are rather of a special character, and manifest themselves most strongly, as we shall see hereafter, at particular periods in Vegetable life (§ 274).—All organised bodies, as already explained, are liable to continual disintegration, even whilst they are most actively engaged in performing the actions of life; in fact, a succession of organs whose individual duration is short, but whose functional energy is great, seems necessary for the maintenance of the life of the more permanent parts of the organism (CHAP. III., Sect. 1). The necessary result of this disintegration is decay; and one of the chief products of that decay is carbonic acid. A large quantity of this gas is set free, during the decomposition of almost every kind of organised matter, the carbon of the substance being united with oxygen supplied by the air. Hence we find that the formation and liberation of carbonic acid go-on with great rapidity after death, both in the Plant and in the Animal; its disengagement being but the continuation (so to speak) of that which has been taking place during life. Thus in Plants, so soon as they become unhealthy, the extrication of carbon in the form of carbonic acid takes place in greater amount than its fixation from the carbonic acid of the atmosphere; and the same change normally occurs during the period that precedes the exuviation of the leaves, their tissue being no longer able to perform its characteristic functions, and its incipient decay giving rise to a large increase in the quantity of carbonic acid set free. In some of these cases, it would seem that the carbon of the decomposing tissue unites with the oxygen contained in the fluids of the system, and that carbonic acid is thus generated, the extrication of which contributes to the introduction of fresh oxygen (§ 266): in other instances, however, the oxygen may be more directly derived from the atmosphere.—The other source of demand for Respiration, which is common alike to Plants and to Animals, arises out of the chemical transformations which are always going-on in their systems, as a part of their nutrient operations. These are as yet but very little understood; but enough is known to justify the belief, that in many of them the presence of oxygen is essential, and that carbonic acid is among their products. Examples of such transformations, drawn from the Vegetable kingdom, will be given hereafter (CHAP. VIII., Sect. 2); but it may be remarked in this place, that the

conversion of starch into sugar, a change that takes place in the neighbourhood of many growing parts, is accompanied by the combination of carbon with oxygen to a considerable amount; and that, in general, the production of the vast multitude of organic compounds yielded by Plants, from the substances which are first generated by them at the expense of the inorganic elements, requires a series of chemical changes, in several of which oxygen is taken-in and carbonic acid given forth. Although the number of organic compounds generated by Animals is much less than that which we find in Plants, yet there can be no doubt, from a comparison of their atomic constitution, that oxygen must be taken into combination, and carbonic acid given-off, in many of the chemical transformations which take place in the living body; some of the most remarkable of which will be described in their proper place (CHAP. VIII., Sect. 3).—Besides the evolution of carbonic acid and the absorption of oxygen, it would appear that the exposure of the circulating fluid to the air is the means of keeping the *Nitrogen* of the system at its proper standard; this gas being absorbed or exhaled, according as there is a deficiency or a superfluity of it in the fluids of the body (§ 320).

266. The whole series of reactions taking place between the living organism, and the air which surrounds it or which is contained in the water wherein it lives, may be conveniently included under the general term *Aeration.* This aeration would appear to be, like absorption, a change dependent on physical agencies, and occurring in conformity with their laws, when the requisite conditions are supplied by the structures of an organised being, and by the functional alterations which the living state involves.—All gases of different densities, which are not disposed to unite chemically with one another, have a strong tendency to mutual admixture. Thus, if a vessel be partly filled with hydrogen, and partly with carbonic acid, the latter, which is 22 times heavier than the former, will not remain at the bottom, but the two gases will be found in a short time to have uniformly and equably mixed; and it is on this principle that the constitution of the atmosphere is everywhere the same, although the gases which compose it are of different specific gravities. So strong is this tendency to admixture on the part of different gases, that it will take place when a membrane or other porous medium is interposed between them. This interchange, therefore, evidently resembles the endosmose and exosmose of fluids (§ 169); and although the tendency to admixture of the two gases is the fundamental cause of their movement, the nature of the septum has so much influence over the phenomenon, as sometimes to reverse the results. When plaster-of-paris is employed as the medium of diffusion, the exchange will take place with simple relation to the relative densities of the gases; and a general law has been ascertained by Prof. Graham, which applies to all instances,—that the 'replacing' or 'mutual-diffusion' volumes of different gases vary inversely as the square-roots of their densities. Thus, if a tube, closed at one end with a plug of plaster-of-paris, be filled with hydrogen, the gas will soon be entirely removed, and will be replaced by something more than one fourth of its bulk of atmospheric air; the density of hydrogen being about 1-14th that of the atmosphere. But when organic membranes are employed, the result is much influenced by the relative facility with which each gas permeates the septum. Thus carbonic acid passes through moist

bladder much more readily than hydrogen does; and, in consequence, when a bladder of hydrogen is placed in an atmosphere of carbonic acid, a certain quantity of hydrogen will pass out; but a much larger proportion of carbonic acid will enter, so as to distend the bladder even to bursting. Further, it is found that, if a fluid be charged with any gas which it readily absorbs (as, for example, water with carbonic acid), it will speedily part with it when exposed to the attracting influence of another gas, such as atmospheric air; and the more differeut the densities of the two gases, the more rapidly, and with more force, will this take place. As in the former instance, this attraction will go-on with little interruption through a porous membrane; and part of the exterior gas will be absorbed by the fluid (if of a nature to be so imbibed), in place of that which has been removed.

267. These simple phenomena will afford a key to the explanation of the changes which take place in the aeration of the circulating fluid by exposure to air; for it seems a universal fact, that *carbonic acid* existing in that fluid is exhaled, and is replaced by absorbed *oxygen;* and that an exhalation and absorption of *nitrogen* take place in animals, and perhaps also in plants.

2. *Respiration in Plants.*

268. Under the above designation have been associated two distinct changes, both nearly constant throughout the Vegetable kingdom. The atmosphere being the chief source whence Carbon is supplied to the living plant, the introduction of that element has been confounded with the contrary change, which is also necessary for the continued health of the structure, and which corresponds exactly with the respiration of Animals. The introduction of carbon is effected by the power which the green surfaces of Plants possess, of decomposing, under the stimulus of light, the carbonic acid contained in the air or in the liquids supplied to them; and of retaining or fixing its carbon, whilst they set free its oxygen. In the *Phanerogamia,* the green surfaces of the leaves, and other appendages to the axis, are those by which this fixation of carbon, which may be considered as a process of alimentation, is chiefly, if not entirely effected; and where, as in the *Cactus* tribe, the leaves are deficient, but the stems are succulent and their surfaces green, it is obvious that these last perform the same function. In the *Ferns, Mosses,* &c. there is the same separation of parts as in the Flowering plants; and the process is here also, without doubt, performed by the green parts of the surface. Of the inferior *Cryptogamia,* however, we know very little. The *Fungi* would not seem to depend upon the atmosphere for any part of their supply of carbon, which is altogether furnished by their peculiar aliment (§ 121); and these plants scarcely ever present any green surface, and flourish most in situations to which light has but little access. The same may be said of the *Cuscuta* (dodder) and other leafless parasitic plants of more complex structure, that live upon the prepared juices they derive from the plant to which they attach themselves. There can be no doubt that *Lichens* ordinarily obtain the carbon which enters into their structure, entirely from the atmosphere; and, that the *Algæ* are supported, in like manner, by the carbonic acid contained in the circumambient water; but experiments are yet wanting to ascertain the precise conditions under which its assimilation is effected. Few Lichens have any green surfaces;

and although many of the Algæ are very brilliantly coloured, yet we find them occasionally existing at such depths, as make it difficult to believe that light is the only stimulus under which they can attain this appearance. The simpler forms of Algæ, especially the *Confervæ,* which inhabit fresh water, appear to exercise an important influence in maintaining it in a state fit for the support of animal life; since it seems probable that they absorb the products of the decomposition of that foul matter by which all ponds and streams are constantly being polluted, and at the same time yield a supply of oxygen to the water. It is a notorious fact that Fishes are never so healthy in reservoirs destitute of aquatic plants, as in ponds and streams in which these abound.

269. The entire mass of Vegetation upon the surface of the globe, is thus mainly dependent upon the minute proportion of carbonic acid contained in the Atmosphere, which is not above 5 parts in 10,000. This seems to be as much as Plants in general, under the feeble illumination which those of them are liable to receive, whose 'habitat' is in variable climates, could advantageously make use of; and a larger proportion would probably have been injurious to them, as well as to Animals. But it has been ascertained by direct experiment, that Plants will thrive in an atmosphere containing six or eight per cent. of carbonic acid, or even more, so long as they are exposed to strong sun-light; and it would appear that in climates where the solar light is less obscured by clouds than it is in our own, the growth of plants may be favoured by an unusual supply of this alimentary substance. Thus the floating islands which are constantly being formed on the lake Solfatara in Italy, exhibit a striking example of the luxuriance of cryptogamic vegetation in an atmosphere impregnated with carbonic acid. These islands consist chiefly of Confervæ and other simple cellular plants, which are copiously supplied with nutriment by the carbonic acid that is constantly escaping from the bottom of the lake, with a violence which gives to the water an appearance of ebullition.* Dr. Schleiden mentions that the vegetation around the springs in the valley of Gottingen, which abound in carbonic acid, is very rich and luxuriant; appearing several weeks earlier in spring, and continuing much later in autumn, than at other spots in the same district.†—A very ingenious hypothesis has been raised by M. Brongniart upon the fact, that an increased quantity of carbon may, under particular circumstances, be assimilated by Vegetables. He supposes that, at the epoch of the growth of those enormous primeval forests which supplied the materials of the coal-formation, the atmosphere was highly charged with carbonic acid, as well as with humidity; and that from this source, the Ferns, Lycopodiaceæ, and Coniferæ of that era were enabled to attain their gigantic development. He imagines that they not only thus converted into organised products an immense amount of carbonic acid, which had been previously liberated by some changes in the mineral world, but that, by removing it from the atmosphere, they prepared the earth for the residence of the higher classes of Animals. The hypothesis is a very interesting one, and well deserves consideration. It may be regarded as an almost absolute certainty, that the whole of the carbon now solidified in the coal-deposits of various ages, must have previously existed in

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* Sir H. Davy's "Consolations in Travel," 3rd ed. p. 116.

† "Wiegman's Archiv." Bd. iii. 1838.

the atmosphere; and if we were acquainted with the extent of these, it would be a simple matter of computation to determine, whether, if all this carbon were reconverted into carbonic acid, it would sensibly affect the proportion of that ingredient in the atmosphere.—The recent experiments of Dr. Daubeny* to a certain extent justify the hypothesis of M. Brongniart, by showing that the existing Plants and Animals most allied to those of the Carboniferous period can exist without injury in an atmosphere containing nearly 5 per cent. of carbonic acid; and if such a difference of climate then prevailed (in consequence either of a different distribution of land and water, or of the internal heat of the globe), as would enable the solar rays to act with more constancy and power than they do in Britain at the present time, there seems no reason for asserting that such *might* not have been the case.†

270. The change which, strictly speaking, constitutes the *Respiration* of Vegetables, is not, like that we have been describing, an occasional one; but is constantly taking place during the whole life of the plant, and appears to be more immediately necessary to its healthy existence. This consists in the disengagement of the superfluous carbon of the system, either by combination with the oxygen of the air, or (which is more likely) by replacing with carbonic acid the oxygen that has been absorbed from it; and it does not cease by day, by night, in sunshine, or in shade. If the function be checked, the plant soon dies,—as when placed in an atmosphere with a large proportion of carbonic acid, and without the stimulus of light which enables it to decompose the deleterious gas. Plants which are being 'etiolated' by the want of light, absolutely diminish in the *weight* of their solid contents, owing to the continued excretion of carbon by the respiratory process, although their *bulk* may be much increased by the absorption of water; and if the proportion of carbonic acid in the surrounding air be augmented by its accumulation, they become sickly and die, from the impediment to their respiration. The parallel, therefore, between Plants and Animals appears to be complete, as regards the influence of carbon upon their growth; for to both it is deleterious when breathed, while to both it is invigorating when introduced through the digestive system as food; and whenever Plants, or parts of Plants, derive their nutriment, like Animals, from organic compounds already prepared for them, there do we find the true respiratory process

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* "Report of the British Association" for 1849; p. 56.

† The Author would suggest it as a point worthy of further consideration, whether there may not have been a special relation between the luxuriant growth of the plants that furnish those carbonaceous deposits, which are found especially to be intercalated amongst the Carboniferous, Oolitic, Wealden, and Cretaceous formations; and the deposit of those vast calcareous beds with which they are so remarkably associated. The latter, there is strong reason to believe, are almost entirely of *animal* origin; the carbonate of lime having been drawn by Zoophytes, Echinoderms, and Mollusks, from the waters of the ocean, just as the carbon of the vegetation of these periods was drawn from the carbonic acid of the atmosphere. Now if we imagine that during the progress of those deposits, there was an unusual discharge of carbonate of lime, held in solution by free carbonic acid, by submarine springs issuing from the interior of the earth (like the Solfatara and other calcareous springs, which furnish the 'travertine' deposits, and at the same time promote the growth of plants, at the present day), we seem to have a probable account of the extraordinary abundance of carbonate of lime in the ocean-waters, and of carbonic acid in the atmosphere, at those periods; since the greater part of the latter would have escaped into the air, so soon as it became free to do so by the removal of the pressure which previously restrained it.

taking place, without the counterbalancing fixation of carbon as aliment. This is the case, for example, with Fungi in general; it is the case, too, with the leafless Phanerogamic parasites, which draw their materials from the elaborated juices of other plants, instead of preparing them for themselves (§ 352); it is the case also with the growing embryo, whose food is derived from the store laid-up in the seed, and whose action upon the air is contrary to that of the developed plant, until it has exhausted this store, and has unfolded its leaves to the light so as to take in fresh carbon from the atmosphere; it is the case, again, with all the growing parts which derive their nutriment from the leaves (not being themselves able to decompose carbonic acid), and especially with the flowers; and it is the case, too, even with the leaves themselves, when their functional activity is diminishing, and the decomposing changes in their tissue are commencing.

271. It becomes a question of much interest, to determine the relative amounts of carbon thus absorbed and excreted by Vegetables. Since a large part of the solid material of their tissues is derived from the atmosphere, it is evident that the whole quantity of carbonic acid in the air must be diminished by their growth; but as a certain proportion of that carbonic acid is taken-in by the roots, which are supplied with it through the absorbent agency of the soil (§ 120), the agency of the leaves requires to be tested by experiment. Such experiments have been repeatedly made by very careful and experienced observers; and the general result of them is, that, so long as the leaves continue in healthy action, and are exposed to the influence of light, they are actively engaged in taking-in carbon from the atmosphere;* and that, when entire plants, consisting not only of leaves, but of stems and other parts, are confined in the same portion of air, day and night, and are duly supplied with carbonic acid gas during sunshine, they will go on adding to the proportion of oxygen present, so long as they continue healthy; the slight diminution of oxygen and increase of carbonic acid which take place during the night, bearing no considerable ratio to the degree in which the opposite effect occurs by day.† The balance of nutrition, therefore, between the Animal and Vegetable kingdoms, is thus maintained in a very perfect and interesting manner.

272. With regard to the changes effected by vegetation upon the principal constituent of the atmosphere—Nitrogen—no very certain or definite statement can be made. Although this element enters largely into the composition of Plants, there seems reason to believe that all which they require is derived by them, not directly from the atmosphere, but by the decomposition of the ammonia absorbed by the soil, and taken-up in solution by the roots (§ 120); indeed proof is wanting that the free nitrogen of the air has any concern with vegetable respiration; for the few experiments which have been performed with express view to this subject, lead to the belief that azote is as frequently exhaled as absorbed.

273. In the *Fungi* among *Cryptogamia*, however, and in the 'leafless

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* See the experiments of Mr. Pepys in the "Philosophical Transactions" for 1843, p. 329.

† See Dr. Daubeny's letter to Prof. Lindley, in his "Introduction to Botany," Vol. ii. p. 297.

parasites' (such as the tribe of *Orobancheæ*) among *Phanerogamia*, we have examples of the performance of the true respiratory process, without the antagonizing action of the alimentative; the only change which the growth of these plants induces in the surrounding air, being the replacement of its oxygen by carbonic acid. Thus, from the experiments of Marcet upon Fungi, it appeared that growing Agarics absorbed from the air a large quantity of oxygen; a portion of which appears to combine with the carbon of the plant, and thus to form the carbonic acid which replaces it; whilst the remainder seems to be retained in its structure. The recent experiments of M. Lory upon the respiration of the Orobancheæ* are peculiarly interesting. He found that in every stage of their vegetation, all the parts of these plants, whether they are exposed to solar light, or whether they are kept in the dark, absorb oxygen and give out carbonic acid; the volume of the carbonic acid generated being nearly equal to that of the oxygen which disappears. But that the production of carbonic acid is not a result of a mere union of carbon excreted by the plant, with atmospheric oxygen, but takes place in the interior of the plant as a part of the changes in which its growth consists, appears from the fact, that the disengagement continues for a time when the plants are surrounded by an atmosphere of pure hydrogen. (A parallel fact will hereafter be cited in regard to the respiration of Animals, § 319.) The amount of carbonic acid exhaled is augmented by warmth, which increases the activity of the nutrient operations; and, as in other plants, it is peculiarly great during the period of flowering. The contrast between the action of one of these leafless parasites upon the atmosphere, and that of the plants from which they draw their nutriment, was curiously displayed by placing in two receivers of the same capacity, a portion of the stem of an *Orobanche*, and a portion of the leafy stem of the *Teucrium* on which it grew, each piece being of the same weight; the atmosphere surrounding them was composed of six volumes of common air mingled with one of carbonic acid; and they were exposed to light from 9 A.M. until 3 P.M. of the succeeding day. At the end of this time, the atmosphere of the jar containing the Teucrium did not present a trace of carbonic acid, whilst that in which the Orobanche had been immersed exhibited such an augmentation of carbonic acid, that whilst its original proportion to the oxygen was as 20 to 25, it was then as 36 to 9.—The explanation of this difference is doubtless to be found in the mode in which parasitic plants obtain their nourishment. Being supported, like Animals, upon organic compounds that have been already elaborated by agency of other Plants, they are entirely destitute of the power of decomposing the atmospheric carbonic acid for the purpose of alimentation; and the sole change which they produce in the surrounding air, is of the same kind with the respiration of animals. As already remarked, there is every reason to believe that the same change takes place in *all other* Plants, and that carbonic acid is continually given-off from their *interior*, whilst oxygen is absorbed; although this is masked by the opposite change, which is effected by their *green surfaces* during the influence of light upon them. For so soon as the light ceases to act upon the latter, the respiratory change makes itself manifest; and it has been shown by the experiments of Saussure, that through the *dark portions* of plants, this change is continually taking place.

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* "Annales des Sciences Naturelles," 3e Sér., Botan., Tom viii., p. 158.

274. Further, there are certain processes in the life of all Phanerogamia, in which the function of Respiration seems to go on with remarkable activity, and in which its manifestation is not concealed by the converse operation. One of these is *Germination*, or the development of the young plant from seed, which requires that the starch laid-up by the parent for the support of the embryo should be converted into sugar, the latter being the form in which it is applied to the purposes of nutrition. This conversion involves the liberation of a quantity of carbon, which is disengaged by means of its combination with the oxygen of the surrounding atmosphere; and the young plant may then be regarded as living under the same conditions as the parasitic tribes just referred-to, its nutriment being supplied to it without the necessity for the alimentative operation which it will be afterwards required to perform. Germination takes place most readily in the dark, since the extrication of carbon, which is the most essential part of the change, would be antagonised by the influence of light. The young plant is, therefore, much in the condition of one which is being 'etiolated;' and it is accordingly found that, during the early period of germination, the weight of the solid contents of the seed diminishes considerably, though its bulk increases by the absorption of moisture. This is its state until the *cotyledons*, or seed-leaves, have arrived at the surface, and temporarily perform the functions of leaves. It is an interesting fact that, after many trials, germination has been found to take place most readily in an atmosphere consisting of 1 part oxygen and 3 parts nitrogen, which is nearly the proportion of the air we breathe. If the quantity of oxygen be much increased, the carbon of the ovule is abstracted too rapidly, and the young plant is feeble; if the proportion be too small, carbon is not lost in sufficient quantity, and the young plant is scarcely capable of being roused into life.—The changes which take place during *Flowering*, are very similar to those occurring in germination. A large quantity of oxygen is converted into carbonic acid by the action of the flower; and it is believed that the starch, previously contained in the *disk* or receptacle, is changed by this process into saccharine matter adapted for the nutrition of the pollen and young ovules, the superfluous portion flowing off in the form of honey. It is remarkable that this analogy between germination and flowering holds good, not only in their products, but in the conditions essential to their activity. Neither will commence except in a moderately warm temperature; both require moisture, for flowers will not open unless well supplied with ascending sap; and the presence of oxygen is in each case necessary. It has been well ascertained that the carbonisation of the air bears a direct relation to the development of the glandular disk, and that it is principally effected by the essential parts of the flower, or organs of fructification. Thus, Saussure found that the *Arum Italicum*, whilst in bud, consumed in twenty-four hours 5 or 6 times its own volume of oxygen; during the expansion of the flower, 30 times; and during its withering, 5 times. When the floral envelopes were removed, the quantity of oxygen consumed by the remaining parts was much greater in proportion to their volume. In one instance, the sexual apparatus of the Arum Italicum

consumed in twenty-four hours 132 times its bulk of oxygen. Saussure also observed that double flowers, in which petals replace sexual organs, vitiate the air much less than single flowers in which the sexual organs are perfect. (See also § 365).—The same is the case, again, during the development of leaf-buds from parts in which (as in the tuber of the Potato) a supply of starchy matter has been laid up as the material for their evolution, until they are so far expanded that they can obtain carbon from the atmosphere. Here, too, the growing bud is in the condition of a parasite, being supported upon materials provided for it by other agencies than its own; and here, again, we find that the conversion of the starch into sugar is the process with which the production of carbonic acid appears to be chiefly connected.

275. Besides the means of aeration which the transmission of the nutritive fluid to the external surface affords, the more highly organised Plants seem to have the power of admitting air into cavities existing in the leaves (especially beneath their inferior cuticle, Fig. 156), through their *stomata;* and in this manner a much larger extent of membrane is exposed to its influence. The peculiar organisation which is probably subservient to this purpose, will be hereafter described (§§ 325, 326) under the head of *exhalation,* for which function it appears more particularly designed. But, superadded to this, we find in the Phanerogamia a system of tubes apparently intended to connect the interior of the structure with the external air. These are the *spiral vessels,* which, in their perfect form, are seldom found to contain any but gaseous fluids. In Exogens they are usually confined to the 'medullary sheath' immediately surrounding the pith; in Endogens they are more universally distributed through the stem, forming part of every bundle of fibro-vascular tissue. In each case, however, they traverse the stem in such a manner as to enter the leaves through their footstalks; and they seem to communicate with the intercellular passages, and, through their medium, if not more directly (as some have supposed), with the external air. A curious analogy exists between these respiratory tubes and the *tracheæ* of Insects (§ 302); and although their exact office is not fully ascertained, there can be little doubt that they contribute in some way to the aeration of the internal fluids. It has been found that they contain a larger quantity of oxygen, by 7 or 8 per cent., than that which exists in the atmosphere.—In a great number of the aquatic tribes, both among the simpler and the more highly organised plants, we find cavities expressly adapted for the inclusion of air; but these would seem designed rather to give buoyancy to the structure, than to take any share in the Respiratory function. The air which they contain, however, is seldom identical in composition with that of the atmosphere.

276. Regarding the progressive evolution of the Respiratory system in Plants, much might here be said, which will perhaps be more advantageously deferred to the account of their general development (CHAP. XI). It may be remarked, however, that the early form of the embryo of the Flowering-plants resembles in its want of special organs, the simple vegetation of the cellular Cryptogamia, although it differs in regard to the mode in which nutriment is supplied; the latter deriving it by their unassisted powers from the surrounding elements, whilst the former is provided with it by the parent. At the first period of the germination

of the seed, a close analogy exists, as we have seen, between the growing embryo and the tribe of Fungi. Both are specially supplied with nutriment, which is prepared in the one case by its parent, and in the other by the decay of animal or vegetable matter; both are developed most rapidly when supplied with warmth and moisture, and in the absence of light; and both liberate carbon to a large amount, without assimilating any from the atmosphere. By the time, however, that the cotyledons have risen to the surface and acquired a green colour, the plant has advanced a stage in its growth, and as to its respiratory system has now attained the level of the Marchantia (§ 27), possessing, like it, stomata and intercellular spaces, but being destitute of spiral vessels. These do not appear until true leaves are evolved; and by the time that this last stage in the development has taken place, the cotyledons, which may be regarded as temporary respiratory organs, decay away.—When we have traced the evolution of the respiratory system of Animals in a similar manner, we shall observe a most interesting correspondence between the consecutive phenomena, as they occur in the two kingdoms respectively.

3. *Respiration in Animals.*

277. The dependence of the life of Animals upon the constant performance of the Respiratory function, is more immediate than that of Plants; and this arises, not merely from the circumstance that there are sources of demand for oxygen and of production of carbonic acid in the former, which do not exist in the latter; but also from the fact, that from those which are common to both (§ 265), the amount of carbonic acid generated, as well as of oxygen required, is far larger in the Animal than in the Plant. The more active are the organic functions, and the softer and more prone to decomposition are the tissues, the more considerable will be that constant decay to which all organised fabrics are exposed, even during life: and thus in 'warm-blooded' animals, the high temperature of the body, which favours the vital activity of its component organs, and causes them to *live fast*, will accelerate their decay, and will hence give rise to a more rapid production of carbonic acid and to a greater demand for oxygen; whilst in 'cold-blooded' animals, so long as the temperature of their bodies is low, the 'waste' of the tissues from this source is kept down, their *rate of life* being comparatively *slow*. But when the temperature of the Reptile is raised by external heat nearer the level of that of the Mammal, its need for respiration increases, owing to the augmented waste of its tissues. When, on the other hand, the warm-blooded Mammal is reduced, in the state of hybernation, to the level of the cold-blooded Reptile, the waste of its tissues diminishes to such an extent, as to require but a very small exertion of the respiratory process to get rid of the carbonic acid which is one of its chief products. And in those animals which are capable of retaining their vitality when frozen, or when their tissues are completely dried-up, the decomposition is for the time entirely suspended, and consequently there is no carbonic acid to be set free.

278. But another source of Carbonic acid to be set free by the Respiratory process, and one which is peculiar to Animals, consists in the rapid changes which take place in the Muscular and Nervous tissues, during the period of their activity. Every development of muscular

force or of nervous power is accompanied by a destructive change in a certain amount of tissue, to which change the presence of Oxygen is essential; and one of the products of the union of oxygen with the elements of the Nervous and Muscular substances, is carbonic acid. Hence it may be stated as a general principle, that the peculiar waste of these substances, which is a condition of their functional activity, and which is altogether distinct from the general slow decay that is common to them with other tissues, is another source of the generation of carbonic acid, and of the demand for oxygen in the animal body; and that the amount of the one gas produced, and of the other gas required, will consequently depend upon the degree in which these tissues are exercised. In such animals as are chiefly made-up of the organs of vegetative life, in whose bodies the nervous and muscular tissues form but a very small part, and in whose tranquil plant-like existence there is but very little demand upon the exercise of their functions, the quantity of carbonic acid thus liberated will be extremely small, and the dependence upon a supply of oxygen by no means close. On the other hand, in animals whose bodies are chiefly composed of muscle, and whose life is an almost ceaseless round of exertion, the quantity of carbonic acid thus liberated is very considerable, and the demand for oxygen is incessant; so that vital activity is speedily suspended, if the respiratory function be not performed.—We are enabled to trace the connection between the amount of nervo-muscular exertion, and the energetic performance of the act of respiration, in the class of Insects, better than in any other. They have no fixed temperature to maintain; and they are consequently not in the condition of warm-blooded animals, in which the quantity of carbonic acid set-free is kept-up to a more regular standard by the provision to be presently noticed. On the other hand, they are pre-eminent among all animals in the energy of their muscular power, as related to the bulk of their bodies, so that the waste of muscular tissue during their state of activity must be very great; and we shall hereafter find that the amount of carbonic acid generated in a given time bears a close correspondence with this (§ 322). Among Reptiles, also, the degree of nervo-muscular activity, as of the vital energy in general, bears a constant relation to the elevation of the temperature of the body; so that the demand for respiration from both sources is *increased* by external warmth (§ 323).

279. Besides these sources of demand for Respiration, which are common to all Animals, there is another, which appears to be peculiar to the two highest classes, Birds and Mammals. These are capable of maintaining a constantly-elevated temperature, so long as they are supplied with a proper amount of appropriate food; and their power of doing so (save when the oxygenation of the 'waste' of the tissues is of itself sufficient to generate the requisite amount of heat) is dependent upon the *direct* combination of certain elements of the food with the oxygen of the air, by a process analogous to combustion (§ 129). The quantity of carbonic acid that is thus generated, seems to vary considerably in different animals, and in different states of the same individual: but the principal source of difference lies in variations of external temperature; for the energy of the Respiration increases with its diminution, since more heat must then be generated; and *diminishes* when an increase

of external warmth renders the production of heat within the body less necessary to sustain its temperature. Whenever the temperature of the surrounding medium is below that of the body, if a sufficient supply of food be not furnished and the store of fat be exhausted, the animal dies of cold (§ 116).

280. To recapitulate, then; the sources of the production of Carbonic acid, and of the demand for Oxygen, in the Animal body, are fourfold.—1. The continual decay of the tissues, which is common to all living organised bodies; which is retarded by cold and dryness, and accelerated by warmth and moisture; which takes place with increased rapidity at the approach of death, whether this affect the body at large, or only an individual part; and which goes on unchecked when the actions of nutrition have ceased altogether.—2. The various changes in composition that take place in the fluids and tissues in the progress of their organic construction, many of which involve a liberation of carbon and a higher oxygenation.—3. The destructive metamorphosis which is the very condition of the activity of the Nervous and Muscular tissues, and which therefore bears a direct relation to the degree in which they are exerted.—4. The direct conversion of the hydro-carbonaceous materials of the food into carbonic acid; which is peculiar to warm-blooded animals; and which varies in quantity, in accordance with the amount of heat to be generated.

281. The process of aeration is accomplished, chiefly if not entirely, through the medium of the *fluids* of the body; but the nature of the fluid which is subservient to this purpose varies greatly in different classes of animals, as does also the method employed. We find, indeed, in many instances, that no *special* instrumentality is required; the aeration of the fluids being sufficiently provided-for, by their exposure to the surrounding medium through the thin membrane which forms their external integument, or through its prolongation into their internal cavities; and the renewal of the stratum of that medium in contact with their surface, being accomplished by actions that are more directly subservient to other purposes in the economy.—When the special organs appropriated to the performance of this function in the principal tribes of the Animal kingdom, are brought into comparison with each other, they appear at first sight so very different, that a superficial observer would hardly trace any relation between them (§§ 8, 109). A little reflection, however, will show, that all their forms are reducible to the simple element of which the respiratory organs are constructed throughout the Vegetable kingdom; namely, an extension of the external surface, peculiarly adapted, by its permeability to gases, for the interchange of ingredients between the circulating fluid spread out on one side of it, and the aerating medium which is in contact with the other. Considered, therefore, under this 'instrumental' character, there is a complete 'unity' amongst them all; but when considered with reference to the general plan of structure, we find them to be 'homologically' diverse. Thus, the extension may take place from very different parts of the surface, so that its connections with other organs may be altogether dissimilar in the several classes of Animals. Again, it usually takes place internally or externally, according as the animal is to be an inhabitant of the air or of the waters. In animals modified for atmospheric respiration, the air enters the system to meet the blood: a peculiar set of movements,

more or less complicated, being appointed for its constant renewal by successive inhalation and expulsion. In those adapted to an aquatic residence, a different plan is usually followed. The small quantity of air contained in the water, is all that the respiratory system employs; and it would have been a useless expenditure of muscular exertion, to have provided means for the constant inspiration and expiration of a large amount of so dense a fluid. In all the higher aquatic animals, therefore, the aerating surface is extended outwardly, instead of being prolonged inwards; and the blood is propelled through it so as to come into relation with the surrounding medium, the portion of which in apposition with it is continually being renewed, either by the natural movements of the animal, or by others more expressly contrived for the purpose. In the higher Radiata and the lower Articulata, however, we meet with a peculiar apparatus for introducing water from without into the interior of the body, and for causing it to perform a kind of circulation through a system of canals more or less extensively distributed; the apparatus subservient to this operation has been recently designated the *aquiferous* or *water-vascular system.*—The relation between some of the most diverse forms of these organs will, perhaps, be made more apparent by a simple diagram. Let A B represent the general external surface of the body; then at *a* is shown the character of a simple *outward* extension of it, forming a foliaceous gill, such as is seen in the lower Crustacea; and in like manner, *b* may represent a simple *internal* prolongation or reflexion, such as that which forms the pulmonary sac of the air-breathing Gasteropods. A higher form of the branchial apparatus is shown at *c*, the respiratory surface being extended by the subdivision of the gill into minute folds or filaments, as we see in Fishes; and a more elevated form of the pulmonary apparatus is seen at *d*, the membranous surface being extended by subdivision of the internal cavity, as we find to be the case especially in Birds and Mammals. Lastly, at *e* is shown a plan of one of the 'pulmonary branchiæ' of the Arachnida, which forms a kind of transition between the two sets of organs; the extent of surface being given by gill-like plications of the membrane lining the interior of a pulmonic cavity.—Putting aside such modifications, however, as are destined to suit the particular conditions under which the function is to be performed, and looking simply at the essential characters of the Respiratory organs, we shall observe, on tracing them upwards through the principal classes of animals, the same gradual specialisation which has been noticed in the other systems; for, beginning with the lowest, it will be seen that the general surface is the organ of

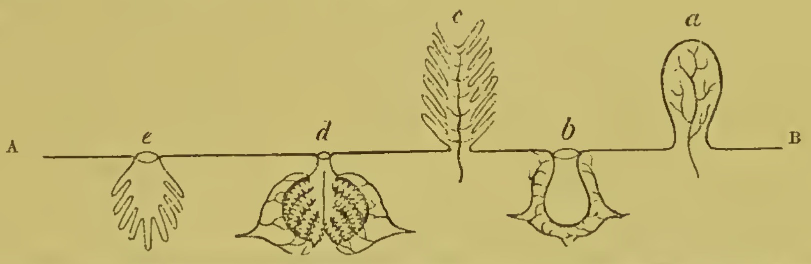

Diagram illustrating different forms of *Respiratory Apparatus*:—*a*, simple leaf-like gill; *b*, simple respiratory sac; *c*, divided gill; *d*, divided sac; *e*, pulmonary branchia of Spider.

respiration as well as of other functions; whilst, in the highest, the aeration of the blood is almost entirely effected in one central apparatus adapted to it alone, although the general surface is not altogether destitute of participation in it.

282. In the simpler *Protozoa*, there is no other fluid to be aerated than that which is contained in each independent cell; and this stands in the same direct relation to the water-atmosphere which bathes its exterior, as is borne by the fluid-contents of the component cells of the highest organism, to the blood-current which brings to them the oxygen they require and carries-off their excrementitious carbonic acid. It may be presumed, on the general principles already stated, that the active *Infusoria* will require a greater amount of respiratory change than the sluggish *Rhozopoda;* and this is provided for them by the very instrumentality which confers upon them their peculiar activity, namely, the *ciliary action*, which either propels them through the water they inhabit, or produces currents in the fluid in immediate contact with their bodies. This same instrumentality,* in the composite *Sponges*, maintains a current in the system of ramifying canals that extends through their interior; a system in which we may be said to have the first indication of a gastro-vascular cavity, a 'water-vascular' or 'aquiferous' system, and a circulating apparatus, not yet differentiated from each other. The fluid which circulates in the Sponge is obviously sea-water, holding in suspension or in solution those minute particles, at whose expense the growth of the component cells of the organism takes place; but it evidently serves also for the aeration of their contents, and also conveys away their excrementitious products.

283. The provision made in *Zoophytes* and *Acalephæ* for the performance of the respiratory function, is not essentially elevated above that which suffices in Sponges. We have seen that these animals possess no other circulating fluid than the chymous product of digestion, which, mingled with sea-water, is transmitted into the prolongations of the polype-stomachs through the absorbent stem and branches of the Hydraform Zoophytes, into the perigastric spaces of the Actiniform and Alcyonian polypes (and their extensions through the composite fabrics of which they form part), and into the gastro-vascular canals of the Acalephæ. This 'chymaqueous fluid,' as it may be termed, will serve to aerate the fluids contained in the tissues of the interior of the body, when it is freshly introduced from without; but if it be long retained within these cavities, it will itself require fresh aeration. It is kept in continual movement within them, by the action of the cilia which usually clothe their surfaces; and it is not improbable that the flux and reflux of this fluid which has been observed within the tentacula of Actiniæ,† like the movement which may be perceived in the contents of the gastro-vascular canals that are distributed near the margin of the disk of Medusæ, is especially destined for its aeration, by exposing it to the circumambient water through a thin intervening septum. It seems not improbable, moreover, that the orifices which certainly exist at the points of the tentacles

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* See the observations of Mr. Bowerbank on the Ciliary movement in *Grantia compressa*, in "Transact. of Microsc. Soc.," Vol. III., p. 137; and those of Dr. Dobie, in "Goodsir's Annals of Physiology," No. II.

† See Dr. Sharpey's account of this movement, in Art. 'Cilia,' "Cyclop. of Anat. and Physiol.," Vol. I., p. 614.

of many species (at least) of Actiniform polypes,[*] and the (so-called) anal pores at the margin of the disk in Medusæ, may serve to introduce fresh supplies of water from without, and to give exit to that which has already become effete, thus foreshadowing the special water-vascular system of higher animals. In some species of Actinia, indeed, the integument of other parts appears to be fenestrated, so that the animal can take-in or eject water through apertures which it has the power of opening or closing; and this can scarcely be for any other purpose than that of respiration.[†]

284. The new relations which the digestive apparatus acquires in *Echinodermata* to the 'general cavity of the body,' involve, as we have seen, a complete differentiation between the chymous contents of the former and the 'chylaqueous fluid' of the perigastric cavity, which here appears to serve, in great part at least, the purposes which are answered in higher animals by the blood (§ 215). Accordingly we find that it is for the aeration of this fluid, that the chief part of those special arrangements are made, which we meet-with under various forms in this class. It was formerly believed that the water in which the Echinoderms live, has free access to the general cavity of their bodies; but this is certainly not the case in regard to some of them, and it is very doubtful whether it occurs in any.—The simplest provision for respiration in this class is presented by the *Sipunculida*, which form a connecting link with the Articulated series. The viscera occupy but a small part of the general cavity of the body, and this is filled with a corpusculated fluid, which may be seen (in some of the smaller semi-transparent species) to perform a continual 'cyclosis,' passing along the parietes of the body from before backwards as far as the proboscis, and then returning to the posterior extremity along the parietes of the intestine. It is probable that this movement is sustained by ciliary action; and while it doubtless serves to convey nutriment to the tissues which the fluid is thus made to bathe, its chief purpose seems likely to be the aeration of the chylaqueous fluid, by bringing it as near as possible to the circumambient water, the skin being so fenestrated at intervals, by the deficiency of the muscular parietes, that only a thin membranous layer separates the two fluids at these points. The chylaqueous fluid is also transmitted into the cephalic tentacula of these animals, which, although essentially prehensile in their character, may also contribute to its aeration, being ciliated both within and without.—In the *Asteriada* we observe an immense number of short,

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[*] The Author cannot but feel much surprise that so many Anatomists of high eminence should still doubt or even deny the existence of apertures at the extremities of the tentacula of Actiniæ. Nothing is more common than to see these animals ejecting minute streams of water from their tentacula, when their bodies are compressed in the attempt to detach them from their base; and it is generally not at all difficult to recognise the apertures, and the sphincter that surrounds them, with the assistance of the microscope. It is possible that such openings may be wanting in some species. (See Hollard in "Ann. des Sci. Nat.," 3e Sér., Tom. XV., p. 269.)

[†] The existence of these apertures has been denied, like that of the tentacular pores, because they were not apparent in the particular species examined. They are probably more frequently deficient than the tentacular pores; but the following testimony seems most explicit as to their existence in some species at least:—"The water in *Actinia crassicornis* and its allies is often ejected in a small stream from the perforated tubercles of their skin, and with such a degree of force that the jet will rise to a height of not less than four inches." (Dr. Johnston's "British Zoophytes," Vol. I., p. 187.)

conical, membranous tubes, passing between the pieces of the shelly framework, and projecting externally in little tufts; these (which were formerly, but erroneously supposed to be perforated at their extremities) are really branchiæ for the aeration of the chylaqueous fluid which passes freely into them, and is moved to and fro by the action of cilia lining their interior, as in the tentacula of Actiniæ.* Besides this, we find a system of vessels, which, though adapted to a special purpose in the economy of the animal, namely, the protrusion of the cirrhi, is probably subservient to respiration also. This consists of a central ring around the mouth, which is furnished with numerous pedunculated vesicles, apparently contractile; from this ring proceed five principal trunks along the five ambulacra; and these trunks seem to communicate with the double rows of vesicles (Fig. 37, *e*) from which the tubular cirrhi are sent forth, that serve as organs of prehension to these animals. The fluid contained in these tubes and vessels appears, from the observations of M. de Quatrefages and Dr. T. Williams, to be of the same nature with the fluid of the general cavity; and it cannot be questioned that, when projected into the cirrhi, it must undergo an aerating change from its relation to the surrounding medium. There would seem to be no special provision for the aeration of the (supposed) blood of these animals, which, not being distributed to the external surface of the body, can only obtain oxygen either from the fluid introduced into the digestive cavity, or from the chylaqueous fluid that bathes the trunks in which it circulates.—The respiration of the *Echinida* seems to be carried-on upon a plan essentially the same; except that the branchial cæca, instead of being dispersed over the general surface of the body, are collected into ten bundles, which pass through the flexible membrane surrounding the mouth. The apparatus for projecting the cirrhi is here very highly developed; these appendages, when fully extended, being often several inches in length, so that the vesicles at their bases (Fig. 95, *k*) are required to be of considerable size.—In the *Holothurida*, however, a far more complicated set of provisions for respiration is found. In the first place, the muscular walls of the general cavity of the body are fenestrated, like those of the Sipunculida, so that the chylaqueous fluid can be exposed to the aerating influence of the surrounding water through the skin alone. Like the shell of the Echinida, again, they are perforated with cirrhi, in connection with which the usual vascular apparatus is developed. Round the mouth is found a beautiful circle of tentacula (Fig. 40, *o*), which are probably at once prehensile and branchial; the parietes of these are furnished with true blood-vessels from the oral ring with which the large contractile vesicle (Fig. 40, *p*) is connected, whilst their hollow axes are filled with chylaqueous fluid from the general cavity of the body. But we find in this group a true *aquiferous* or *water-vascular* system, which, though long considered anomalous, is now found to have its homologues in an extensive group of the lower Articulata. This is the 'respiratory tree,' which, in its higher grades of development extends from the cloaca into the visceral cavity in a beautiful arborescent form on each side of the body (Fig. 40, *r*, *r*), though in the lower it is a simple undivided sac. Both the stem and branches of this organ contain distinct circular and longitudinal muscular fibres, which contract on being irritated, and which expel the water it contains, through its cloacal orifice, at tolerably regular intervals (such as once, twice, or three times in a minute), its re-introduction being apparently accomplished by ciliary action. The contraction of the muscular fibres of the external integument may probably assist in the expulsory action; but it is not required, since the respiratory movement continues even after the sac has been laid open. One of the branches of the 'respiratory tree' lies in close contiguity with the alimentary canal, so that the blood in the respiratory plexus (Fig. 40, *v r*) of the mesenteric system of vessels, will be brought into immediate relation with the aerating fluid introduced by it; the other branch lies in nearer proximity to the parietes of the body, and its respiratory action is probably exercised rather upon the 'fluid of the general cavity.'*

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* Sharpey, Op. cit., p. 616.

285. It is among the Vermiform members of the Articulated series, that we find the 'water-vascular' system acquiring its highest development. But it will be desirable first to study it under the simpler form it presents in the *Rotifera*, which have no rudiment of a sanguiferous system, the chylaqueous fluid of the general cavity of the body being the medium alike for conveying nutriment to the solid tissues, and for effecting respiratory changes in them. On either side of the body of these animals, there is usually found a long flexuous tube (Fig. 96, *i*, *i*), which extends from a contractile vesicle (common to both) that opens into the cloaca, towards the anterior region of the body, where it frequently subdivides into branches, one of which may arch over towards the opposite side, and inosculate with a corresponding branch from its tube. Attached to each of these tubes are a number of peculiar organs (usually from two to eight on each side) in which a trembling movement is seen, very like that of a flickering flame; these appear to be pear-shaped sacs, attached by hollow stalks to the main tube, having a long cilium in the interior of each, attached by one extremity to the interior of the sac, and vibrating with a quick undulatory motion in its cavity; and there can be no doubt that their purpose is to keep-up a continual movement in the contents of the aquiferous tubes.†—Similar lateral vessels, furnished internally with

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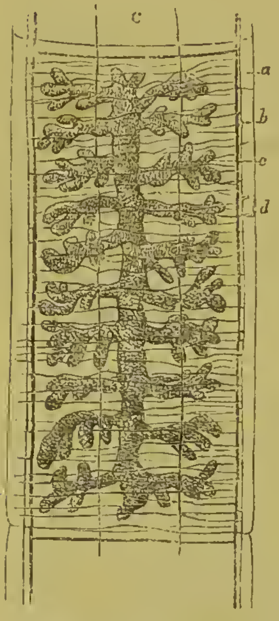
* On the respiration of the Echinodermata, see especially the Memoir of M. de Quatrefages 'Sur la Cavité générale du Corps des Invertébrés,' in "Ann. des Sci. Nat.," 3e Sér., Zool., Tom. XIV.; and the less sound but more detailed Memoirs of Dr. T. Williams, 'On the Blood-proper and the Chylaqueous Fluid of Invertebrated Animals,' in "Philos. Transact.," 1852; and 'On the Mechanism of Aquatic Respiration,' &c., in "Ann. of Nat. Hist.," 2nd Ser., Vols. 12, 13.—The whole of the vascular system connected with the cirrhi is regarded by Von Siebold and others as belonging to his 'Water-vascular' or 'aquiferous' system; but the Author does not see adequate reason for so considering it, and thinks that it much more fairly ranks as a special apparatus exclusively belonging to this class. That it is at first developed, as the observations of Prof. Müller have shown, by an inversion of the external integument, and is for some time in free connection with the exterior, being only shut-off when its internal ramifications have been extensively developed, is no argument against the latter view; whilst it is much in favour of it, and against the determination of Von Siebold, that a true water-vascular system exists, concurrently with the system of the cirrhi, in the Holothurida,—the group that presents the nearest approach to the Vermiform tribes, in which this system is most characteristically displayed.

† See Huxley 'On *Lacinularia Socialis*,' in "Transact. of Microsc. Soc.," New Series, Vol. I. Mr. Huxley's description of these organs differs from that previously given by other observers, who have supposed that these pyriform sacs had apertures of communication with the general cavity of the body; but the Author has much confidence that Mr. Huxley's account is the correct one.

vibratile cilia, and often ramifying more minutely (especially in the head and anterior part of the body) are found in many of that group of Vermiform animals, clothed over the whole surface of their bodies with cilia, to which the designation *Turbellaria* has of late been given. These vessels have been commonly regarded as *sanguiferous;* and it is certain that the fluid which they contain is sometimes coloured, like the (so-called) blood of Annelida;[*] but it is certain, also, that they have usually, probably always, external orifices, these being sometimes numerous. In *Nais,* instead of actually opening into the cloaca, one set of them comes into close relation to the rectum, the interior of which is richly ciliated; thus reminding us of the parallel distribution of the tracheal system in the larvæ of *Libellulidæ* (§ 305). In fact, it seems not improbable that the 'water-vascular' system of the lower Articulata (which are all aquatic) is the homologue of the tracheal system of the air-breathing Myriapods and Insects; and that, where it does not convey water directly introduced from without, the fluid which it contains is specially subservient to respiration, establishing a communication between the aerating surface and the tissues of the body generally. There is an almost complete absence among the *Turbellariæ,* of any more special respiratory organs. The whole tegument of the body, being soft and clothed with cilia, is probably subservient to this function; but there are occasionally to be observed about the head (as in *Nemertes*) particular groups of cilia longer and more closely set than the rest, reminding us of the 'wheels' of the Rotifera.

FIG. 136.



Segment of *Tænia solium;* displaying, *a, b,* the larger and smaller longitudinal trunks which pass along each side; *c,* ovary; *d,* genital orifice.

286. This 'aquiferous' system of vessels presents its greatest complexity and most elevated character in the group of *Entozoa;* whilst at the same time, there are certain types even of that class, in which it exists under its most simple and least doubtful aspect. It is only, in fact, by tracing it through its principal forms and gradations, that the real import of some parts of this system can be ascertained. In the *Cestoid* worms, we find four principal canals, two on each side (Fig. 136, *a, b*), running along the body at or near the margins of the segments, and connected together by transverse branches; these anastomose with one another freely in the head, those of the opposite sides being generally connected by an arched canal; whilst at the opposite extremity they all terminate in a single contractile sac opening externally. Besides these trunks (of which the two larger, *a,* have been considered as a double alimentary canal), there is a superficial system of vessels more minutely distributed, which has been regarded as sanguiferous; but these may be traced into connection with the preceding, and their parietes are furnished

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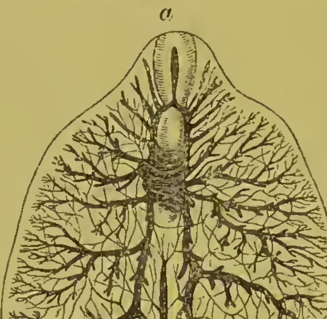
[*] See the Memoir of M. de Quatrefages, 'Sur les Némertiens,' in "Ann. des Sci. Nat.," 3e Sér. Zool., Tom. VI.

with vibratile cilia, which keep-up a movement of their contents. There is, then, no true sanguiferous system in the Cestoid Worms, any more than there is an alimentary canal; both being replaced by the direct absorption of the nutritious juices from without, in a state ready for assimilation. Yet it is probable that, as in the cases last cited, the 'water-vascular' system contains some other fluid than pure water; and it may even serve, as Prof. Van Beneden has suggested, for a urinary apparatus. The fluid contents of these vessels, whatever their nature may be, are kept in motion partly by ciliary action in their interior, and partly by the contractility of their walls; the former method seems to prevail in the smaller trunks, the latter in the large.—In the *Trematode* Worms, we find a regular gradation from what is unquestionably a 'water-vascular' system homologous with that of the Cestoidea, to an apparatus which nearly approaches the reputed sanguiferous system of the Annelida. One of its most interesting forms is that presented by the *Distoma tereticolle;* in which we find an elongated contractile canal, terminating posteriorly in an external orifice, giving off two contractile trunks, which pass along the two sides of the body without any change of dimension, and unite in an arch above the mouth. The fluid of these vessels is colourless, and contains some minute corpuscles. But besides these, there are a considerable number of smaller trunks, giving-off branches that form a network resembling that shown in Fig. 137; these trunks, however, have been distinctly found by M. Van Beneden to discharge themselves into the two principal lateral canals, so that they must be considered as forming one system with them, although the fluid which they contain is coloured. This system of vessels, therefore, although usually described as sanguiferous, cannot be properly regarded in that light; and it is obvious, that even when (as happens in the *Echinorhynci,* which are closely allied to the Trematoda) there are no pale, ciliated, non-contractile aquiferous vessels, terminating in an external orifice, but only red, non-ciliated, contractile vessels, which cannot be traced into connection with the exterior, we must abstain from regarding the latter as a true 'sanguiferous' system, since they are obviously but an offset (so to speak) from the 'aquiferous,' specially developed in this particular group of animals.—The nature of the vascular system in the *Nematoid* worms (Fig. 52) has not yet been

Fig. 137.



Anatomy of *Fasciola hepatica* (Distoma hepaticum) enlarged, showing the ramifications of the digestive cavity through the whole body of the animal, and the vascular network connected with a median trunk; *a*, the mouth.

made out; but there appears strong ground for the belief that in this order also, what has been usually regarded as a sanguiferous system really belongs to the 'aquiferous' type.*

287. An arrangement of a different kind, but one that seems referrible to the 'water-vascular' system of inferior Articulata, is found in the Leech and Earthworm, which, with their allies, constitute the *Monœcious* group of Annelids. In the medicinal *Leech*, there is found on either side of the posterior part of the body a series of seventeen pairs of sacculi, lying between the digestive cæca, and opening by narrow external orifices; although these were long ago considered as respiratory organs, yet they have been of late more generally regarded as organs of secretion;† their homological character, however, as a 'water-vascular' system, appears to be demonstrated by the existence of intermediate forms, which connect it with the aquiferous system of Entozoa. Thus in *Branchiobdella* there are but two pairs of external orifices, one at the anterior and the other at the posterior extremity of the middle third of the body; each of these leads to a trunk, which, after dilating into an ampulla, gives off several tortuous canals, the lining of which is ciliated. In the *Earthworm*, again, there is found in each segment, and on either side of the digestive tube, an enteroid vessel which returns upon itself, and which is lined with cilia; and in other Lumbricidæ, these vessels have cæcal terminations in the general cavity of the body, furnished like the water-vessels of Rotifera (§ 285), with long cilia.‡—Nothing similar to this has been found among the branchiferous Annelida; and it would seem as if the water-vascular system were superseded in them by the apparatus provided for aquatic respiration, which will be hereafter described (§ 292).—The close resemblance which seems to exist between the multiple sacculi of the Leech, and the air-sacs of the lower Myriapoda (§ 301), strengthens the reasons already advanced (§ 285), for regarding the 'water-vascular' system as the real homologue of the tracheal system of Myriapods and Insects. And if the suggestion already thrown out (§ 219), respecting the real nature of the supposed sanguiferous system of Annelida, should prove well-founded, this also would find its parallel in the *closed* tracheal apparatus of certain Insect-larvæ (§ 305), which is connected, like it, with a branchial apparatus; the difference between the two being that the latter contains and distributes *air*, whilst the former is filled with an *aeriferous* fluid, which can scarcely be called blood, the distribution of *nutritive* materials being accomplished in both cases by the fluid of the 'general cavity of the body.'

288. *Branchial Respiration.*—In by far the larger proportion of

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* See on this most important subject, the treatise on "Les Vers Cestoides," by Prof. Van Beneden (Bruxelles, 1850); and his Note 'Sur l'appareil circulatoire des Trématodes,' in "Ann. des Sci. Nat.," 3e Sér., Zool., Tom. XVII. Also Siebold, 'Ueber den Generation's wechsel der Cestoden,' in "Siebold and Kölliker's Zeitschrift," 1850; Wagener, in "Müller's Archiv.," 1851; and "Brit. and For. Med. Chir. Rev.," Vol. X., pp. 324—6.—The Author is informed by his friend Mr. Huxley, that he has recently detected in the *Ascaris* (a Nematoid Entozoon) of the Plaice, two non-ciliated lateral contractile vessels, extending the whole length of the body, and united over the œsophagus by a transverse branch which appeared to open externally.

† See Quatrefages, in "Ann. des Sci. Nat.," 3e Sér., Zool., Tom. XIV., p. 297.

‡ These terminations have been affirmed by good observers to be sometimes *open*. See Leydig on *Branchiobdella*, "Zeitschrift für Wissen. Zool.," Band III., and Gegenbaur on the *Earthworm*, Ibid., Band IV. Mr. Huxley has also seen them in *Nais*.

aquatic animals, including nearly the whole of the Molluscous sub-kingdom, the classes of Annelida and Crustacea among the Articulated, with Fishes and Batrachia (at least in their early or larval condition) among the Vertebrated, we find the circulating fluid transmitted for aeration to external appendages, which are disposed in the various forms of leaflets, fringes, tufts, &c., and the water in contact with which is continually renewed, sometimes by the action of the cilia that clothe their surfaces, sometimes by a muscular apparatus specially adapted for the purpose. These *branchiæ*, however, are not always apparent externally; being frequently enclosed in some extension of the integument, which either simply covers them in, or which forms a special chamber for their reception, with orifices of entrance and of exit for the water that is conveyed over the respiratory surface.—As it is in the *Molluscous* sub-kingdom that this plan of respiration is most characteristically developed, we shall first examine the principal forms of the branchial apparatus which it presents; and shall then proceed to notice its chief peculiarities in Articulated and in Vertebrated animals.

289. The lowest division of this series, however,—namely, the group of *Bryozoa*,—can scarcely be said to possess any special respiratory apparatus, the degradation of their circulating system extending itself also to this; still, the aeration of the nutritious fluid that occupies their visceral cavity seems to be provided-for, by its transmission along channels in the interior of their ciliated tentacula (Fig. 49, D, *b*, *b*); and it has also been observed that the wide pharynx is sometimes dilated with water, which is expelled again without passing into the stomach, as if it had been taken-in for the aeration of the fluids of the body.*—In the class of *Tunicata*, of which the Bryozoa may be regarded as a degraded form, we find (save in a few aberrant genera) a highly-specialized apparatus for the performance of the respiratory function. This apparatus is always connected with the *entrance* to the alimentary canal; and the currents of water set in motion by the cilia that cover it, serve (like those impelled by the ciliated crown of the Bryozoa) the double purpose of bringing fresh supplies of food to the digestive cavity, and of water to the aerating surface. Two types of conformation, that are at first sight very different, present themselves in the respiratory apparatus of this class; the most simple being that of the *Salpidæ*, the most elaborate that of the ordinary *Ascidians*. In the Salpidæ we find the large cavity that occupies the greater part of the interior of the body, to be traversed by a riband-like fold of its lining membrane (Fig. 122, A, *d*), which stretches obliquely from its anterior attachment a little behind the oral orifice (*a*), to its posterior attachment to the visceral nucleus, between the œsophageal orifice and the rectum; thus partially dividing the cavity into two parts, an anterior or pharyngeal, and a posterior or cloacal. The anterior is really the dilated pharynx, which, in an early stage of the development of these animals, extends directly (as in Bryozoa) from the oral orifice to the entrance of the œsophagus; a condition which is permanently retained in the curious *Appendicularia*. The posterior portion, on the other hand, is really a distended cloaca, formed by an inflection of the second tunic round the anal orifice; this inflection commences in the embryo as a simple depression of the surface, and then

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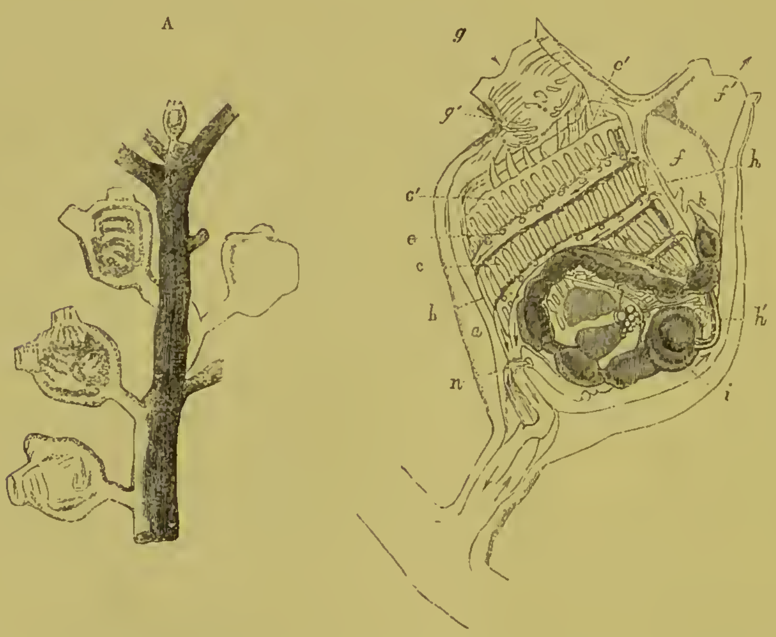
* See Dr. A. Farre 'On the Cilobrachiate Polypi,' in "Philos. Transact.," 1837, p. 407.

extends inwards so as to meet the pharyngeal sac, with which it comes to communicate by a large aperture on each side; and this gradually widens, until the whole forms one respiratory sac, of which the alimentary canal (both of whose orifices are received into it) seems but a diverticulum. The branchial lamella, formed by the united lining membranes of the pharyngeal and cloacal cavities, is traversed by an extension of the great 'sinus-system,' which passes-in between its two layers; in some species, only a single grand sinus runs through it; but in others there is a complex system of vascular ramifications, extending from this sinus over its surface, as shown in Fig. 122. It is beset with cilia on either side of its free edge; and by the action of these a current of water is continually drawn-in through the oral orifice, and propelled backwards, part of it entering the œsophagus, but another part at once passing into the cloacal portion of the cavity, to be expelled through the anal orifice or vent (*b*). Although this organ is undoubtedly the special instrument of respiration, yet it can scarcely be questioned that the whole lining membrane of the cavity is also subservient to the same action, especially where this is minutely vascular throughout, as shown in Fig. 122, B. Ciliary action is not the only—perhaps not the principal—means of renewing the water required for respiratory purposes in the Salpidæ; for they execute rhythmical movements of alternate

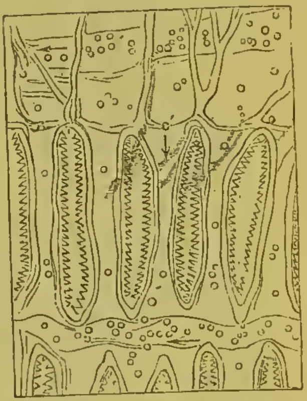
FIG. 138.



A, Group of *Perophora* (enlarged), growing from a common stalk:—B, single *Perophora*; *a*, test; *b*, inner sac; *c*, branchial sac, attached to the inner sac along the line *c′ c′*; *e, e*, finger-like processes projecting inwards; *f*, cavity between test and internal coat; *f′*, anal orifice or funnel; *g*, oral orifice; *g′*, oral tentacula; *h*, downward stream of food; *h′*, œsophagus; *i*, stomach; *k*, vent; *l*, ovary (?); *n*, vessels connecting the circulation in the body with that in the stalk.

contraction and dilatation, the former being accomplished by the instrumentality of their muscular bands, the latter by the elasticity of the 'test' when the muscular action ceases; and in this manner the water received into the cavity, being prevented from returning through the oral orifice by a bilabiate valve which closes it, is ejected through the anal, with a force that drives the animal in the opposite direction.—In all the tribes which make-up the group of *Ascidians*, on the other hand, the dilated pharynx (Fig. 138, B, *c*) is completely embraced by the inflected cloacal sac, save along the dorsal line, where the great thoracic sinus intervenes; and the communication between them is established by a number of vertical slits, arranged in regular rows, and fringed with cilia very closely set together (Fig. 139). This peculiar conformation, like that of the Salpidæ, is only attained as embryonic development advances; for the cloacal sac, which commences as a superficial depression in the position of the anal orifice, is gradually inflected inwards, until it almost entirely surrounds the pharynx; and in the pharyngeal wall thus formed by the coalescence of the two contiguous membranes, one aperture is formed after another, until the entire series is completed. The spaces between the rows of slits are occupied by thickened transverse bars; and these contain extensions of the sinus-system, along which the circulating fluid passes between the great sinus which runs vertically along the dorsal margin and the other which passes along the ventral margin. The spaces between the slits of the same row are not thus thickened, but they seem to contain extensions of the sinus-system, as globules of blood may be seen to move in them. From the transverse bars, digitiform processes are occasionally sent into the cavity; and the oral orifice is usually fringed with a set of tentacula projecting inwards. The use of these would appear to be, to receive impressions from particles drawn-in by the respiratory current, whose presence is unsuitable; these impressions serving to excite a contraction of the muscular sac, whereby a gush of water is expelled through one or both orifices,—an action analogous to that of coughing in the higher animals. No such muscular movements are concerned, however, in sustaining the ordinary respiratory current; this being entirely kept-up by the action of the cilia, here so abundantly distributed. The greater part of the water thus drawn-in, is at once transmitted through the slits in the branchial sac, into the cloaca, whence it is ejected by the vent; the solid particles fit for food, however, are retained, and are gradually carried-down to the entrance of the œsophagus: and the small stream of water which passes with them into the alimentary canal, is discharged through the intestine into the cloaca, so as to pass-out by the vent.—Notwithstanding the apparent difference between these two plans, they are really reducible to a common type; as is shown alike by the history of their development, and by the occurrence of intermediate forms, such as *Doliolum* and *Pyrosoma*, which establish the transition from one to the other. The curious *Appendicularia* permanently resembles, both in its general structure and in the conformation of its respiratory apparatus,

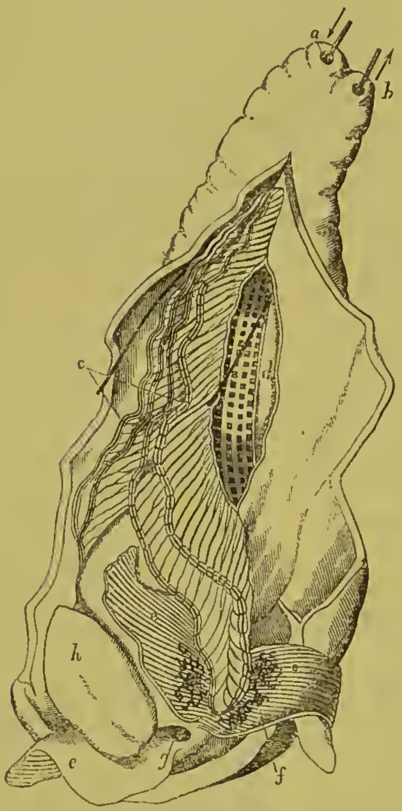
Fig. 139.



Portion of branchial sac of *Perophora*, highly magnified, showing the slits lined with cilia, and the currents of blood flowing between them.

the larvæ of the Ascidians. For it possesses no cloacal cavity, the intestine opening directly on the external surface; the dilated pharynx has therefore no internal communication, save with the alimentary canal; and the water which is taken into it for respiratory purposes, and is not required to pass through the intestinal tube, is ejected again by the oral orifice. Thus, whilst possessing the peculiar conformation of a larval Ascidian (being unattached, and moving freely through the water by a long caudal appendage, like an *Amaroucium* in its early state, Fig. 246), this curious being shows but a very slight departure from the Bryozoic type. For if the tentacular circle of a Bryozoon were to become rudimentary, if the general cavity of its body were to be contracted, by the partial adhesion of its opposite walls, into a sinus-system, and if one portion of this should acquire a contractile coat, we should have all the essential parts of the digestive, circulatory and respiratory apparatuses, nearly in the relations which they actually bear to one another in Appendicularia.*

Fig. 140.



Interior view of *Pholas crispata*, the mantle being laid open along the ventral margin :—*a*, incurrent siphon, and *b*, excurrent siphon, having whalebone probes passed through them into the chambers with which they respectively communicate; *c*, branchial laminæ; *d*, anal chamber laid open, showing four rows of orifices leading to tubes between branchial laminæ; *e*, *e*, labial tentacles; *f*, accumulation of particles of indigo, propelled along the edges of the gills; *g*, oral orifice; *h*, foot.

290. Passing-on now to the *Bivalve* Mollusks, we find that the expansions of the mantle which line the shells of the *Brachiopoda*, and over which the blood is freely distributed, constitute their principal organ of respiration; the surrounding water being freely admitted to the space between the valves, and being probably kept in motion by the agency of the cilia that clothe the 'arms.' In those species in which the shell is perforated by cæcal extensions proceeding from the great sinus-system within each valve to its external surface (§ 236 *note*), it is probable that these, like the papillæ of the Nudibranchiate Gasteropods (§ 291), may serve as an additional means for aerating the blood. As the blood which circulates among the viscera and in the ciliated arms must be brought into aerating relation to the water that is in contact with every part of the

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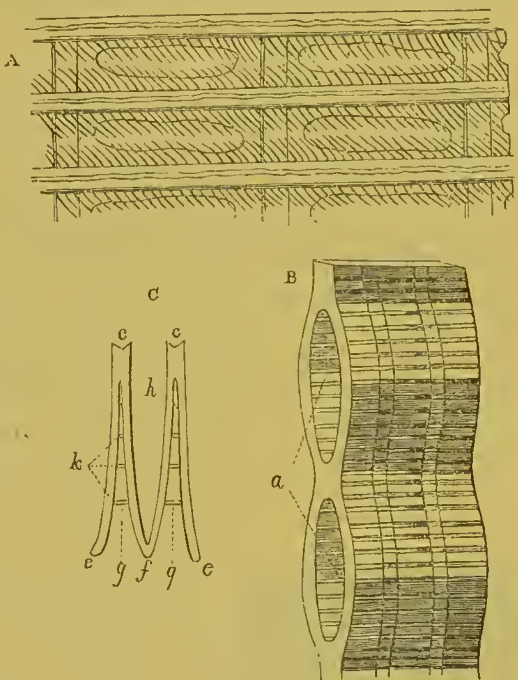
* See the Monograph of Prof. Milne-Edwards, "Sur les Ascidies Composées" (1840); the Memoirs of Mr. Huxley, on the 'Anatomy of Salpa and Pyrosoma,' and on 'Doliolum and Appendicularia,' in "Philos. Transact.," 1851; and the Notice by the same excellent and philosophical observer in the "Report of the British Association," 1852.—A very ingenious idea of the Homology of the Organs of the Tunicata and Polyzoa (Bryozoa) has been put forth by Prof. Allman in the "Transact. of the Roy. Irish Acad.," Vol. XXII.; but the Author agrees with Mr. Huxley in considering this idea to be negatived by the phenomena of development, as observed by Krohn, "Müller's Archiv.," 1852.

thin integument, there seems the less reason for any peculiar specialization of the respiratory apparatus. The *Lingula* (Fig. 82) presents in some degree a transition from this low type, towards the higher condition of the Lamellibranchiate bivalves; its mantle being thrown into plaits or folds, which prefigure *their* lamellated branchiæ.*—In the *Lamellibranchiate* Bivalves, we find the internal surface of the expansions of the mantle that line the valves, to be doubled (as it were) into four riband-like folds (Fig. 140, *c*), which are very minutely supplied with blood-vessels (Fig. 123, F, F), and which are obviously the special organs of aeration, though the general surface of the mantle still doubtless participates in that function. Of the four branchial lamellæ, two are attached to each lobe of the mantle; and each of them consists of two folds of its membrane (as will be seen in Fig. 141, C), which are continuous at its edge (*c*) and are attached at certain points of their contiguous surfaces (*k*), but are separated at others by intervening channels (*g*, *g*), the interval between them being widest at the base. Only one of these laminæ is usually attached (*f*), the borders (*e e*,) of the others being free, so that a probe may be passed between them into the interior spaces (*g*, *g*) between the layers. The structure of these layers varies considerably in the different families of the class; for in some instances they are continuous membranes, perforated (like the branchial sac of the Ascidians) with slits arranged in rows and fringed with cilia, the intervals between which are occupied by blood-channels; whilst in other instances they seem made-up of ciliated bars containing blood-channels, but having few points of union with each other. In either case, however, the effect is the same. The water is propelled over the surface of the branchial lamellæ in a constant stream, by the action of the cilia that border their fissures, whilst the blood is made to traverse the spaces intervening between these fissures, and is thus effectually aerated. The water that has performed this office, passes through the fissures into

FIG. 141.



Branchial apparatus of *Lamellibanchiate* Mollusk:—A, portion of branchial laminæ highly magnified, showing orifices in the meshes of the vascular net-work, fringed with cilia:—B, section of gill-plate, showing two of the tubes formed by the adhesion of its laminæ:—C, ideal section of the two branchiæ of one side; *e c*, free layer of each gill; *f c*, its attached layer; *g g*, spaces between the layers, communicating with the anal chamber; *h*, interval between the contiguous lamellæ; *k k*, bars connecting the two folds of the same lamella.

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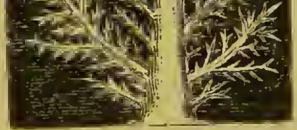
* The term *Palliobranchiata* has been proposed by Prof. Owen as an appropriate designation for this group, being indicative of the performance of the respiratory function by the general surface of the mantle.

the spaces (g, g) between the branchial lamellæ, and is discharged in a stream from the extremity which is nearest the anal outlet. It is only in a comparatively small number of Lamellibranchiata, that the two lobes of the mantle are free (as in the Oyster) along the entire margin of the valves, so that the water can enter at any point; for they are generally found to be more or less united, so that the gills become enclosed within a branchial cavity. There is always a provision, however, for the free access of water from without, by means of two apertures (Fig. 140, a, b), one of which serves for its entrance, and the other for its ejection; and in certain species which burrow deeply in sand, mud, wood, &c., these apertures are furnished with long tubes or siphons reaching to the entrance of the burrow, which are themselves lined by cilia. In the *Pholas* (Fig. 140) and its allies, among which the closure of the mantle-lobes is carried to its fullest extent, the cavity is divided into a branchial and an anal portion, which have no other communication the one with the other than through the fissures in the branchial lamellæ. The two laminæ of each gill are in such close adhesion to each other, that the intrabranchial spaces (Fig. 141, C, g, g) are reduced to a set of parallel tubes (as shown at B C), which open into the anal chamber. Thus the water that enters by the branchial or incurrent siphon (Fig. 140, a), after finding its way through the slits in the branchial lamellæ (shown in Fig. 141, B, and more highly magnified at A), into the intrabranchial tubes, passes at once into the anal chamber, and is discharged by the anal siphon (Fig. 140, b). In its course over the branchiæ, however, it is deprived not merely of its oxygen, but also of whatever alimentary particles it may contain; and these are collected, by a very peculiar adaptation of the ciliary mechanism, on the free edges of each lamina (f), along which they gradually travel to the orifice of the œsophagus (g); as has been shown experimentally by diffusing particles of indigo through the water thus introduced.* As in the Tunicata, the presence of an obnoxious particle will cause its ejection with a jet of water through the branchial orifice; the branchial cavity being forcibly pressed-on by the valves of the shell, which are drawn together by the adductor muscles.

FIG. 142.



One of the arborescent processes, forming the gills of *Doris Johnstoni*, separated and enlarged.

291. The class of *Gasteropoda* is remarkable as being the only one in the entire series of Mollusca, that contains animals adapted for atmospheric respiration. The 'pulmonated' Gasteropods, however, are comparatively few in number; by far the larger proportion of this group being provided with branchiæ, in which their blood is aerated by the contact of water. These branchiæ in many orders form tufts of an arborescent character (Fig. 142), which may be disposed upon various parts of

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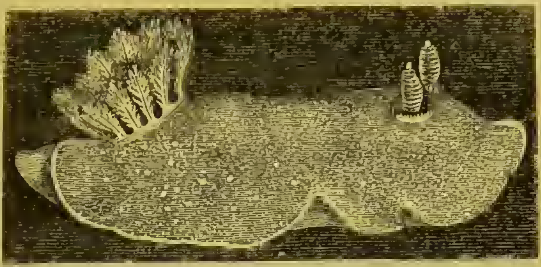
* See especially, upon this subject, Prof. Sharpey's Art. 'Cilia,' in "Cyclop. of Anat. and Physiol.," Vol. I., p. 622; and Messrs. Alder and Hancock, in "Ann. of Nat. Hist.," 2nd Ser., Vol. VIII., 1851, p. 370.—Mr. Clark, in various numbers of the same journal, has endeavoured to prove that water is ordinarily taken-in by the 'pedal gape,' and is discharged by the branchial as well as by the anal siphon. But the Author considers that there is ample evidence that such is not the ordinary course of the current.

FIG. 143.



Doris Johnstoni, showing the tuft of external gills.

the surface of the body, or may be collected into a single cluster (Fig. 143). There can be no doubt that, in the *Nudibranchiate* Mollusks, the general surface of the body takes an important share in the aeration of the blood; and it appears that in some instances it must constitute the principal, or even the sole instrument for the performance of this function, since there is little or no trace of any special respiratory apparatus. We have seen that the former is the case in regard to *Doris;* it being only the blood which has circulated through the liver, kidneys, and ovaria, that is sent to the branchial circlet, whilst the remainder is transmitted for aeration to the skin. In *Eolis* (Fig. 104) and its allies, the skin with its papillæ seems to constitute the only instrument of aeration, no more special provision for this purpose being discoverable; and the whole of its upper and lateral surface, as well as the surface of the papillæ themselves, is clothed with cilia. In some members of this family, the surface is further extended by the peculiar conformation of the papillæ; every one of which is furnished with a sort of membranous frill, across which the blood must pass from the afferent canal in the papilla itself to an efferent vessel that runs along the free margin of the frill, which conveys the blood back to a great trunk-vein that is formed by the meeting of all these papillary vessels.* In most of the other branchiferous Gasteropods, the gills are more or less covered by the shell; and even where this is but little developed, as in the Aplysia, we find it specially devoted to their protection. The order *Pectinibranchiata,* which is the highest and most numerous subdivision of the class, receives its name from the peculiar pectinated or comb-like arrangement of its gills (Fig. 144), which are lodged within a cavity formed by the arching of the mantle behind the head; and into this cavity the water is admitted by a special channel or siphon.—The *Pteropoda* seem to be destitute of any special respiratory organ; their blood being aerated by distribution to the general surface of the mantle, the inner surface of which is minutely vascular.—The highest development of the branchial apparatus presented by the Mollusca, is that which we find in the *Cephalopoda.* In these animals, the gills are very large, especially in the Dibranchiate order (Fig. 125, *o, o*); and they are lodged in a cavity formed by the folding-over of the mantle, to which water is admitted through a wide fissure at the base of the head; whilst the current, after passing over them, is ejected through the funnel (*e*). The respiratory surface is not here covered with vibratile cilia, but the respiratory current is sustained entirely by the alternate contractions and dilatations of the muscular parietes of the cavity; whilst, in the presence of special branchial hearts for the propulsion of the blood through the gills (§ 239), we have another provision for the increased vigour of the respiratory function, required by the active habits of these animals, which present a remarkable contrast to the sluggish inert character of the Molluscous series generally.—In that series, taken as a whole, the respiration is low in its amount. But as their life is chiefly vegetative, as their movements (except in the highest classes) are few and feeble, and as they maintain no independent heat, there is comparatively little need of the interchange which it is the object of the Respiratory process to effect; and they can sustain the complete suspension of it for a long time.

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* See Mr. A. Hancock, on the Anatomy of *Oithona*, in "Ann. of Nat. Hist.," 2nd Ser., Vol. VIII., p. 297.

292. In the classes of *Annelida* and *Crustacea,* which belong to the Articulated series, the respiratory process is carried-on upon a plan very much resembling that which has been just described; the aquatic habitation of these animals involving the necessity of provisions that shall answer the like purposes. Still we find that whilst the structure of the branchiæ is essentially the same in the Articulata as in Mollusca, their form and disposition present many important points of difference; the most remarkable of these being their uniform bilateral symmetry, and longitudinal repetition.—The respiratory organs of the various orders and genera of the Annelida differ greatly, not only as to form and arrangement, but also as to their relations to the circulating apparatus. We have already seen (§ 218) how important a part the 'chylaqueous fluid' of the general cavity of the body performs in the nutrition of the greater number of these animals; and how strong is the probability (§ 219) that the coloured non-corpusculated fluid conveyed by the (supposed) sanguiferous system is not truly *blood,* but serves no other purpose than that of a carrier of oxygen and of carbonic acid between the tissues and the aerating medium. Now in the interior of a large part of the appendages with which these animals are furnished, there are tubular cæcal prolongations from the general cavity of the body, into which the 'chylaqueous fluid' freely passes; and these must be considered as being subservient to the aeration of that fluid, whatever may be their other offices. Into others, nothing but the (so-called) blood is transmitted; and these have distinct afferent and efferent vessels, like the branchiæ of Fishes. In other cases, again, the same appendage contains a provision for the exposure of both fluids. As a general rule, when the branchiæ are sanguiferous only, they are contractile, but are not ciliated; when, on the other hand, they receive the chylaqueous fluid, they are invariably clothed with cilia. The form of the branchial organs varies most remarkably, from a simple conical or filamentous appendage, to a branching tuft, or to an expanded lamina. They are almost invariably repeated in considerable numbers, either on the head, or along the back or sides of the body; it is only in a few rare cases, that they are restricted to its posterior extremity.—In the *Serpulæ* and their allies, constituting the order *Tubicolæ,* the respiratory organs are grouped around the head, forming tufts whose brilliant colours and symmetrical arrangement render them, when fully expanded, most conspicuous and beautiful objects.* Thus in *Sabella unispira* (Fig. 144), they

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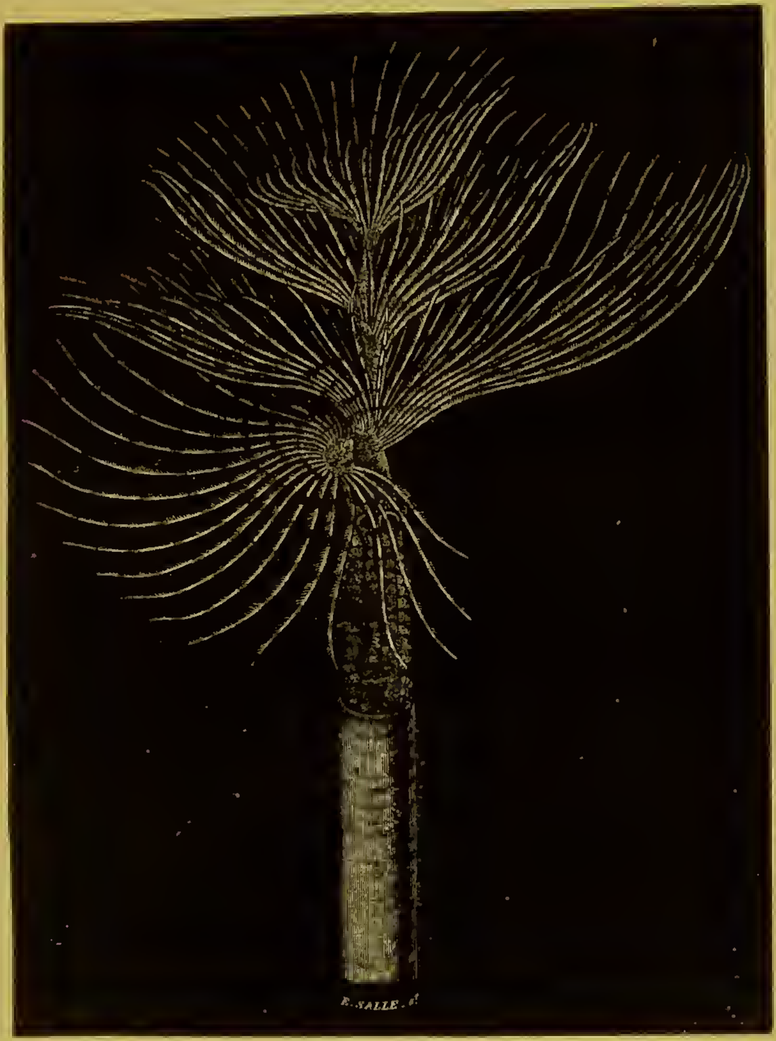
* There are few sights more striking to the observer of nature in tropical regions, than the unexpected view of a bed of coral in shallow water, having its surface scattered with the brilliant tufts of the Serpulæ which have formed their habitations in it; the glowing and variegated tints of which, when lighted up by the mid-day sun, and contrasted with the sombre hues of the surrounding rocks, present an appearance compared to which the most beautiful garden of carnations (which flower the animals much resemble in form) sinks into insignificance.

are disposed spirally around a central column; and each straight process has a double row of lesser filiform appendages, every one of which contains an afferent and an efferent blood-vessel, and is richly ciliated on its under surface. Although so contractile that they can be readily folded-up and withdrawn into their tube, the branchial filaments are not used for prehension; the food of these animals being obtained from the currents of

Fig. 144.



Sabella unispira.

water brought to their mouths by the cilia which cover the respiratory appendages. In the *Terebella,* on the other hand, the head is furnished with prehensile cirrhi or tentacula (Fig. 113, *b*), which further act as branchiæ for the chylaqueous fluid that passes freely into them: whilst beneath these we find the sanguiferous branchiæ (*k*, *k*), of a beautiful arborescent form, and reddened by the blood that fills them; the former organs are clothed with cilia, whilst the latter are not. In the *Arenicola,* again, the ramose branchiæ which are disposed at regular intervals along the sides of the body (Fig. 115), and which are the sole external organs of respiration, are purely sanguiferous like the proper branchiæ of Terebella; and there is here no distinct provision for the aeration of the chylaqueous fluid, unless this be accomplished through the parietes of the alimentary canal, the wet sand which the animal is perpetually swallowing, serving as an aeriferous medium. In *Eunice* (Fig. 114), again, the branchiæ are purely sanguiferous; but in some allied genera, the chylaqueous fluid also penetrates the loose tissue around the blood-vessels, which are relatively smaller in size; and in *Nephthys* (Fig. 53) the hollow of each branchial process is chiefly occupied by the chylaqueous fluid, in the midst of which a coiled vessel carrying blood is seen to float. In *Syllis*, which is not far removed from the preceding in general structure, the branchial organs are penetrated by chylaqueous fluid alone. A most remarkable provision for the aeration of this fluid is seen in *Branchellion*, a leech-like Annelid provided with two pairs of laminated branchial appendages, an anterior and a posterior, to each segment; for the chylaqueous fluid is conducted to these by a set of vessels with distinct parietes, which form a plexus upon their surface, without, however, any efferent vessels for its return; whilst the blood does not penetrate further than the base of each of the anterior pairs of branchiæ, which contains a dilated contractile vesicle that serves as a heart. Finally, there are several degraded forms of this class, in which there is no special provision for the aeration, either of the chylaqueous fluid, or of the (so-called) blood; the general surface in these worms being capable of affording all the interchange of constituents between the fluids of their bodies and the surrounding medium, which the necessities of their economy require.*—In many animals of this group, as we have seen in the preceding chapter, there are special provisions for the propulsion of the blood through the branchiæ, the feeble contraction of the systemic trunks not affording sufficient power.

293. The higher Articulated classes are, for the most part, adapted to atmospheric respiration, on the plan to be presently explained; but there is one class, that of *Crustacea*, whose respiration is still carried-on through the medium of water. In the suctorial forms of this group, there is no special respiratory apparatus; the general surface being soft enough to admit of the required aeration of the fluids through its own substance, and the animal functions being performed with so little activity, that a very small amount of interchange is required. In the higher orders, however, whose bodies are encased within a harder envelope, a special respiratory organ is almost invariably found. In some of these (as the *Branchiopoda*, Fig. 60), the last joints of all or of the greater number of the legs are flattened-out into membranous surfaces, which appear calculated to permit the influence of the air upon the nutritious fluid that penetrates them, and which, by their incessant strokes upon the water, continually renew the medium in contact with them and with the body generally. Proceeding higher (to the order *Amphipoda*) we find a particular portion only of the extremity, the flabellar appendage, devoted to respiration; but

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* See the Memoirs of M. de Quatrefages on the 'Respiration of the Annelida,' in "Ann. des Sci. Nat.," 3e Sér., Zool., Tom. XIV., p. 290, et seq.; and on the 'Anatomy and Physiology of Branchellion,' Op. Cit., Tom. XVIII., p. 306, et seq. See also the Memoir of Dr. T. Williams, in "Ann. of Nat. Hist.," 2nd Ser., Vol. XII., p. 393, et seq.

this is developed to an increased extent, and the water in contact with its surface is incessantly renovated by currents set in motion by the abdominal members. The next stage in the specialisation of this function, is the restriction of the branchial apparatus (as in the order *Isopoda*) to the abdominal members, which are entirely devoted to it, and cease to have other uses. In a still higher order (*Stomapoda*), the gills have assumed more of the character which they present in Fishes and some Mollusca; the laminated or leaf-like form which they at first possessed, having given place to one in which the surface is greatly extended by minute subdivision into delicate filaments. The most developed form of respiratory apparatus possessed by Crustaceans, is that which exists in Crabs, Lobsters, and other *Decapods* (Figs. 58, 120). In this order, not only is the function thrown upon particular organs entirely set apart for the purpose, but these organs are lodged and protected within a special cavity; and the renewal of the water necessary to their operation is secured by the motion of distinct appendages. This cavity is formed by a reduplication of the external tegument, and is provided with two orifices, one for the introduction and the other for the expulsion of the fluid. Through these orifices a constantly-renewed supply of water is made to pass, by the agency of a large valve-like organ, placed in the efferent canal, which, by its movements, drives a continual current from behind forwards, and thus occasions a constant ingress through the afferent opening; this organ is nothing else than the flabelliform appendage of the second pair of feet-jaws, specially developed to answer this purpose.* The perfect contact of the water with the respiratory surface is further provided-for, by the actions of the flabelliform appendages of other maxillary or ambulatory members, which, in most Decapods, penetrate into the branchial cavity, and incessantly sweep the surface of the branchiæ, apparently for the purpose of combing out their filaments (so to speak) by means of the stiff hairs with which they are furnished.† In those Crustacea which are adapted to live for a time on land, the orifices of the branchial cavity are very small, so that but a trifling amount of evaporation can take place from them; and it appears that, in all the species, the gills can be subservient to aerial as well as to aquatic respiration, provided their surface be kept moist,—the asphyxia of the animals in a dry atmosphere being due to the desiccation of this membrane, and its consequent unfitness for the performance of its functions. There are other species, known as Land-Crabs, which not only live habitually out of water, but are infallibly drowned if kept long immersed in that fluid. The membrane lining their branchial cavities is sometimes disposed in folds, capable of serving as reservoirs for a considerable quantity of water; and sometimes presents a spongy texture equally well adapted for storing-up the fluid, which is necessary to keep the organs of respiration in the state of humidity required for the performance of their functions. Land-crabs are never known to remove far from damp situations; and this humidity may be either derived from the atmosphere, or furnished, as in higher air-breathing animals, by a secretion from the circulating fluid. It can scarcely be doubted that the spongy lining of the branchial cavity in these Crustacea is peculiarly subservient to aerial respiration; and it appears to be owing to the check given to its activity, that land-crabs are drowned when plunged under water.

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* Prof. Milne-Edwards, Art. 'Crustacea,' in "Cyclop. of Anat. and Physiol.," Vol. I,

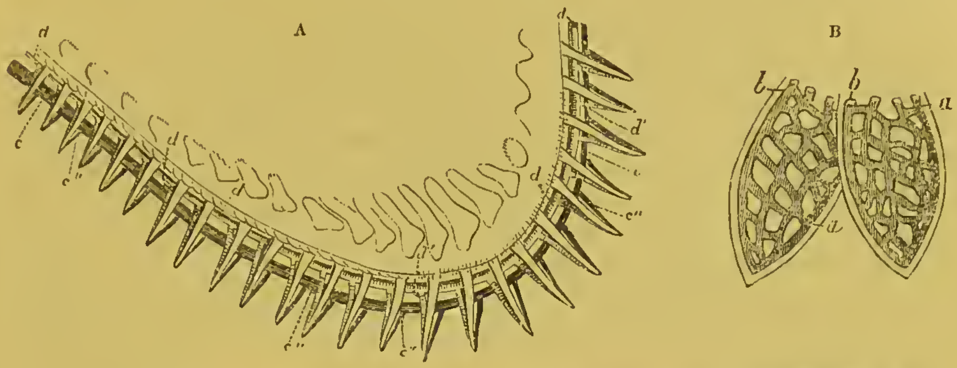
† See Quekett in "Transactions of Microscopical Society," Vol. II., p. 37.

294. The stages in the development of the branchial apparatus of the *Astacus fluviatilis* (Cray-fish) have been so beautifully traced-out by M. Milne-Edwards (op. cit.), in connection with the various forms of the same in adult species of different tribes, that it seems advantageous to notice them here for the sake of ready comparison, rather than to defer the account of them to the general description of the progressive evolution of the system in the embryo of higher animals.—In the earlier periods of embryonic life, no trace of branchiæ can be discovered; so that the embryo may then be considered as on a level with those inferior Crustaceans, whose respiration is entirely carried-on by the general surface. When these organs are first evolved during the process of incubation, they consist of simple laminated expansions, representing the flabelliform appendages of the three pairs of maxillary members, and thus corresponding with the branchial feet of the Branchiopoda. These soon subdivide, and one part assumes a cylindrical form, and seems no longer to belong to the apparatus, whilst branchial filaments begin to appear on the other, which are subsequently prolonged into complete gills; during this interval the thoracic extremities have made their appearance, and they also become furnished with branchial appendages; and thus in possessing respiratory organs which are quite distinct from the instruments of locomotion, but are altogether external, the embryo Decapod corresponds with the higher Stomapoda. At a subsequent period, a narrow groove or furrow is seen along the under edges of the thorax, the margins of which, in no long time, are prolonged so as to meet each other and enclose the gills; openings being left for the entrance and exit of water, which are at first large, but subsequently become contracted to the proper size. It is thus evident that the lining membrane of the cavity, as well as that which covers the filaments of the branchiæ, is but a prolongation of the external tegument.

295. Although the respiratory apparatus in *Fishes* retains the type which characterised it in the inferior aquatic classes, it undergoes a great increase both in extent and importance. In order to keep-up with the rapid advance in the development of the other systems, the respiration requires to be conducted, though by means of an aquatic element, with great velocity and effect. For this purpose, it is not sufficient that Fishes should have merely filamentous tufts hanging loosely at the sides of the neck; but it is requisite that they should possess the means of rapidly and constantly propelling large streams of water over their surface, and of forcing the whole blood of the system through the respiratory apparatus, to be submitted to the action of the air that is contained so scantily in the water. The former of these ends is effected by the connection of the gills with the cavity of the mouth, the muscles of which send a rapid current of water through the branchial passages; and the latter, by the alteration in the position of the heart, which is placed so as to propel the blood through the respiratory organs *before* it proceeds to the system at large (§ 240). The gills in most Fishes are disposed in fringed laminæ, the lamellæ of which are set close together like the barbs of a feather, and are attached on each side of the throat, in double rows,

to the convex margins of four or five long bony or cartilaginous arches (Fig. 145, A), which are suspended from the hyoidean arch. The extent

Fig. 145.



A, Branchial arch of *Fish*, with its blood-vessels; *c c'*, branchial artery, diminishing in size from *c* to *c'*, in proportion as it furnishes the twigs *c'' c''* to the branchial lamellæ; *d d*, the branchial vein, which augments in the same proportion, as it receives the venous twigs *d' d'*.—B, capillary net-work of a pair of leaflets of the gills of the *Eel*:—*a*, *a*, branches of the branchial artery conveying venous blood; *b*, *b*, branches of branchial vein, returning aerated blood. The disappearance of the dark shading in the net-work, as it traverses the gill, is designed to indicate the change in the character of the blood, as it passes from one side to the other.

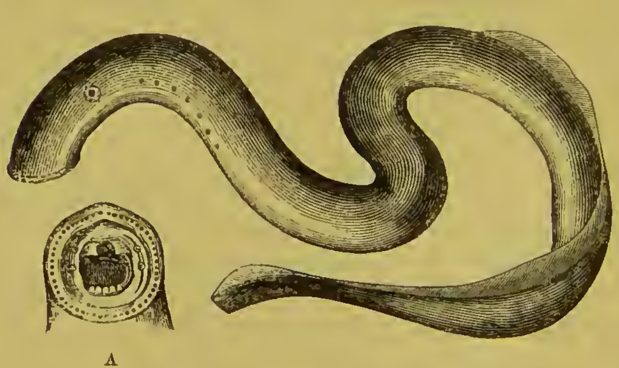
of surface exposed by these gills is very great, and the network of capillaries spread over them is extremely minute (B). In the *Osseous* fishes, the gills are lodged in a capacious chamber, which communicates internally with the pharynx, by a distinct orifice for each interspace between the branchial arches; whilst externally it opens by a single large orifice on each side, which is furnished with a valvular bony *operculum*, that allows free passage to the currents ejected from the mouth, but serves for the protection of the delicate organs beneath it. In the higher *Cartilaginous* fishes, the gill-chamber is more completely subdivided; the branchial lamellæ being attached, not merely at their bases to the branchial arches, but by their opposite extremities to the membrane lining the chamber; and each branchial interspace has its own external orifice for the discharge of the water. We shall hereafter find that the branchial fissures in the neck, which thus form a direct communication between the pharynx and the external surface, may be seen in all the higher Vertebrata at a certain stage of development (§ 316).

296. A curious departure from the ordinary type of the respiratory apparatus of Fishes, which carries us back to the type of the Tunicated Mollusca, presents itself in *Amphioxus*. The oral cavity of this animal opens posteriorly by a large orifice (Fig. 127, *ph*) into a wide pharyngeal cavity (*r r*), the walls of which are strengthened by a sort of cage, formed of delicate, transparent, hair-like, cartilaginous arches, seventy or eighty in number, whilst between these are a series of clefts, the edges of which are fringed with cilia. This pharyngeal sac appears to serve as the principal respiratory apparatus; for a considerable part of the water which is taken in by the action of the oral ciliated lobes, and which enters the pharyngeal orifice, is driven through these slits into the abdominal cavity, from which it makes its exit by the abdominal pore *od;* the remainder passing through the cardiac orifice (*py*) into the digestive cavity. Besides this organ, however, another means of aeration is provided in a set of digitate

prolongations of mucous membrane (*g g*) contained within the cavity of the mouth; these, being copiously supplied with blood and closely set with cilia, and being exposed to the first stream of water as it enters the mouth, are perhaps to be considered (as is urged by Prof. Owen*) as the most efficient part of the respiratory apparatus. The venous blood which has passed through the system is for the most part collected into the posterior part of the great ventral trunk, which is furnished with a pulsatile dilatation close to the posterior extremity of the branchial sac; and from this ventral trunk are given off numerous branches, which pass round the pharynx between its fissures, and discharge themselves into the dorsal trunk *ba*. The anterior continuation of the ventral trunk, which transmits the blood forwards to the head, also conveys it through the vessel *b v* to the ciliated appendages within the mouth, after which it is carried to the dorsal trunk, whence it proceeds to the system generally, together with the blood that has been aerated by passing through the walls of the dilated pharynx.

297. Another remarkable variation is presented in the *Cyclostome* Fishes; in which we find six or seven pairs of gills on each side, and these not attached to cartilaginous arches, but developed as folds from the lining membrane of as many distinct sacculi. To understand the relation between these and the gills of ordinary fishes, we must suppose (as Prof. Owen has remarked†) each compressed sac of the *Myxine* to be split through its plane, and each half to be glued by its outer smooth side to an intermediate septum, which would then support the opposite halves of two distinct sacs; if then these vascular surfaces be prolonged into lamellæ, tufts, or filaments, and an intermediate basis of support be developed, we have the branchial arch of one of the higher cartilaginous Fishes, which is the homologue, not of a single gill-sac, but of the contiguous halves of two distinct gill-sacs, in the Myxine. The first part of this change is seen in the *Lamprey;* in which we also find the branchial sacculi communicating with the pharynx, not directly by a separate fissure for each, but through the medium of a tube which comes off from the pharynx on either side, and conveys the water by a distinct branch to each gill-sac. In most of the Cyclostomi, as in the Lamprey, each sac opens externally at the side of the neck by a separate orifice (Fig. 146); but in the Myxine the efferent current is conveyed by a special tube, which collects it from all the sacculi of one side, and passes backwards to discharge itself near the middle line of the ventral surface; thus present-

Fig. 146.



Lamprey:—A, *its circular suctorial mouth.*

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* "Hunterian Lectures on Comparative Anatomy," Vol. II., p. 254.

† Op. cit., p. 259.

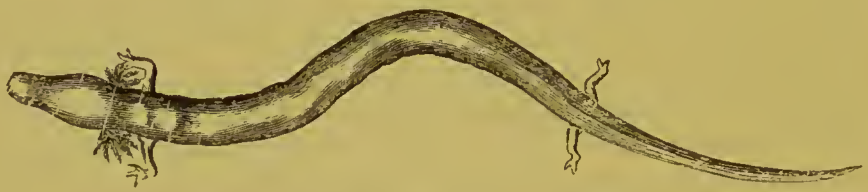
ing a connecting link between the provision for the discharge of the respiratory current in Amphioxus, and that which prevails in ordinary Fishes.—Some even of the Osseous fishes present a departure from the ordinary type, in the prolongation and contraction of the efferent canal; and this is particularly remarkable in the *Eel* tribe, in which we find the two orifices approximating each other on the under side of the neck, until, in *Synbranchus*, they actually meet, so that the respiratory current is discharged from both sides by a single pore on the median line.—During the embryo condition of both the principal divisions of this class, the gills may be seen hanging loosely from the back part of the neck: for, in Osseous fishes, they have attained considerable development, before the prolongation of the integument has been formed into the valve which covers them; and in the Cartilaginous fishes, the branchial openings are at first large, and the filaments of the gills are prolonged much beyond them,—other filaments also, which subsequently disappear altogether, being produced from their edges.

298. The mechanism of Respiration is very complex in Fishes; and is adapted to produce the most effectual aeration which their organs admit of. The mouth is first distended with water; and its muscles are then thrown into contraction, in such a manner as to expel the fluid, through the apertures on either side of the pharynx, into the gill-cavity. At the same time, the bony arches are lifted and separated from each other, by the action of muscles especially adapted to this purpose; so that the gill-fringes may hang freely, and may present no obstacle to the flow of the water between them. When they have been thus bathed with the aerating liquid, and their blood has undergone the necessary change, the water is expelled through the external apertures by muscular pressure; its return to the pharynx being prevented by the valves with which the orifices are furnished. It is well known that most Fishes speedily die when removed from the water; and it can be easily shown that the deficient aeration of the blood is the immediate cause of their death. But as it might have been expected that the atmosphere would exert a much more energetic influence upon the blood contained in the gills, than that which is exercised by the small quantity of air contained in the water, the question naturally arises, how this deficient aeration comes to pass. It is chiefly due to the two following causes;—the drying-up of the membrane of the gills themselves, where it is exposed to the air, so that the aeration of the blood is impeded;—and the flapping-together of the filaments of the gills, which no longer hang loosely and apart, but adhere in such a manner as to prevent the exposure of the greater portion of their surface to the air. Those among ordinary Fishes can live longest out of water, in which the external gill-openings are very small, so that the gill-cavity may be kept full of fluid: but there is a particular family, that of *Labyrinthibranchii*, in which the anterior branchial arches give origin to a curious lamellated apparatus, in whose interspaces water may be retained for a considerable length of time, so as to keep the gills moist; and by this provision, analogous to that which exists in the Land-Crab (§ 293), such fishes are enabled to remain for a considerable time out of water, performing long migrations over land in search of food, and even (it is said) ascending trees.—The respiration of Fishes is much more energetic than that of any of the aquatic Invertebrata; and this is partly

due to the great extension of the surface of the gills, partly to the provision just explained for maintaining a constant flow of fresh water over their surface, and partly to the position of the heart at the base of the main trunk that conveys the blood to the gills, by which the energetic propulsion of that fluid through these organs is secured. Their blood, too, is furnished with red corpuscles, which seem to give important aid in conveying oxygen from the gills to the remote tissues of the body, and in returning the carbonic acid to be excreted. The proportion of these, however, varies considerably in the different species of the class; being very small in those that approach most nearly to the Invertebrata, whilst they are present in large numbers in the blood of certain Fishes, which have great muscular activity, and can maintain a high independent temperature.

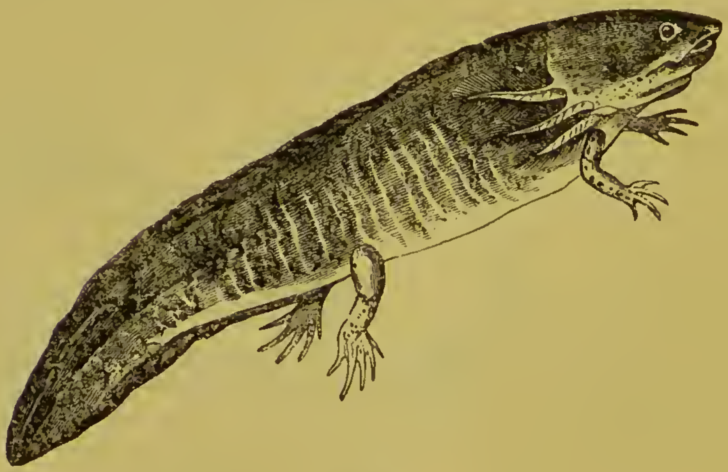
299. The branchial apparatus temporarily possessed by the *larvæ* of the higher *Batrachia*, and persistent in the *Perennibranchiate* division of the same order, is constructed in all essential particulars upon the plan of that of Fishes. In the first instance the branchiæ are external, hanging as tufts from the sides of the neck (Figs. 147, 148); and these external gills, like the branchiæ of Invertebrated animals, are covered with cilia, whose actions are of considerable importance in renewing the stratum of water in contact with them. This state continues in most of the Perennibranchiata through the whole of life; but in the *Amphiuma* and *Menobranchus*, the external gills disappear, without being replaced by internal

Fig. 147.



Proteus Anguineus.

Fig. 148.



Axolotl.

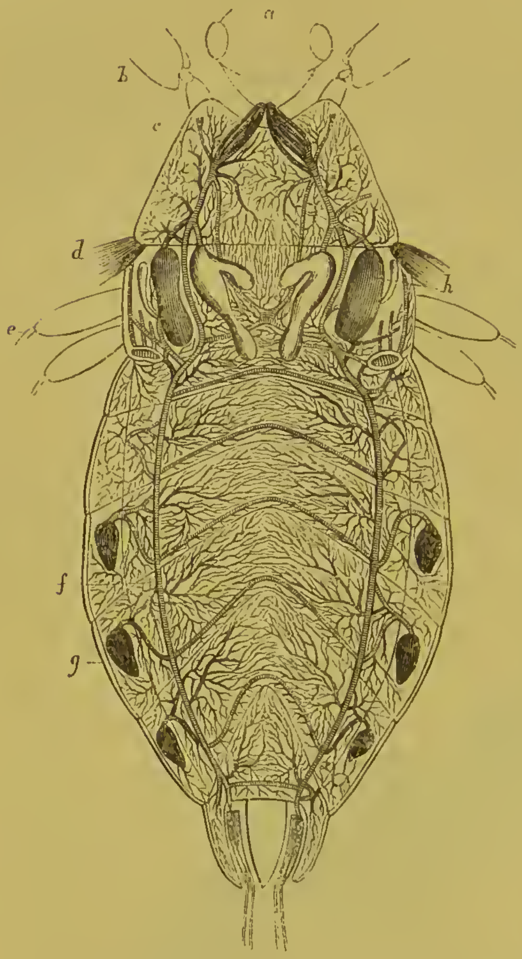
organs of a like kind, and nothing remains of their branchial apparatus, save the fissures leading from the pharynx and the surface of the neck. In those Batrachia, however, whose development proceeds further (as Frogs and Water Newts), the branchiæ are subsequently more or less enclosed by a fold of the skin, which forms a membranous valve, analogous to the bony operculum of Fishes; and in the tadpole of the Frog, the branchial cavity thus formed is closed completely on the right side, the water which has passed through it being ejected through the opening that remains on the left.

300. *Atmospheric Respiration.*—Having thus traced the organs of aquatic respiration, from their simplest and most general, to their most elaborate and most specialised forms, we have to follow the same course with those which are provided for *atmospheric* respiration. None such are met with among the *Radiated* classes, which are all aquatic; and the Pulmonated Gasteropods are the only *Mollusca* which are adapted for breathing air. This group includes not merely the Snails, Slugs, and other terrestrial Gasteropods; but also several, which, although habitually living beneath the water, receive air (taken-in at the surface) into a pulmonic cavity, instead of respiring through the medium of branchiæ. This pulmonic cavity is a simple undivided sac (Fig. 124, *d*, *d*), on the walls of which the blood-vessels are minutely distributed; it lies beneath the dorsal portion of the mantle, and communicates with the external air by a single orifice on the right side of the neck, provided with a sphincter-muscle by which it can be occasionally closed.

301. In a large proportion of the *Articulated* series, however, we find the apparatus for atmospheric respiration presenting a high degree of development; but, like the branchial organs of the lower members of that series, it exhibits a tendency to repetition in successive segments, which is in striking contrast with the conformation just described. What are to be *homologically* considered as the organs of respiration, however, appear in some instances to have little or no connection with the function, as is the case in regard to the air-bladder of Fishes (§ 307). For the sacculi of the Leech and Earthworm (§ 287), which open externally on each side of the body by orifices that correspond in position to the spiracles of Myriapods and Insects, are always found to be full of fluid, and seem rather to be secreting organs, destined to pour forth a watery mucus for the lubrication of the skin, than to be directly concerned in the aeration of the blood (?) or of the chylaqueous fluid of these animals. This seems to be sufficiently provided-for by the cutaneous surface, to which we have seen that the blood is specially transmitted in the Leech (§ 220); but it is only when quite moist, that the skin can thus serve as a respiratory organ; and in maintaining this condition, the secreting sacculi just described are indirectly subservient to this function.—In *Myriapoda*, however, we find a regular transition presented by the respiratory apparatus of the different families, from that just described, to that which is characteristic of Insects; for whilst in the lower *Iulidæ* the spiracles lead only to a double series of sacculi presenting few or no ramifications, the higher members of that group have a set of ramifying *tracheæ*, issuing from each sacculus, and proceeding to the various organs of its own segment; and in the *Scolopendridæ* the tracheal systems of different segments come into connection with each

other by mutual inosculation, some even possessing the two longitudinal canals connecting together the whole series of spiracles and the main trunks of the tracheæ, which we find in Insects. The tracheæ themselves are formed, as in Insects, of two membranes, between which an elastic spiral fibre winds round and round the tube, so as to prevent its cavity from being easily obliterated by compression.

Fig. 149.



Tracheal system of *Nepa* (Water-Scorpion):—*a*, head; *b*, first pair of legs; *c*, first segment of the thorax; *d*, second pair of wings; *e*, second pair of legs; *f*, tracheal trunk; *g*, one of the stigmata; *h*, air-sac.

302. In studying the Respiratory system of *Insects*, we shall have occasion to observe several peculiar modifications which it undergoes for particular purposes, whilst its essential character remains unaltered; and we shall have also an opportunity of noticing the varieties of form and function which the same apparatus may present at different periods of life, and under changes in external conditions. The muscular energy required for the locomotive powers of the perfect Insect, and the general activity of its organic processes, necessarily involve a large amount of communication between the nutritious fluid and the atmosphere; but, on the other hand, the low development of the circulating system would prevent the aeration from being accomplished with sufficient rapidity, by the transmission of the blood through one particular organ. The difficulty is obviated by the introduction of the vivifying agent into every part of the body, by means of a complex and minutely-distributed system of 'tracheæ;' which ramify through even the smallest and most delicate organs, and thus bring the air into immediate relation with all their tissues;* whilst they also dilate in certain parts into sacculi, which sometimes attain a considerable size (Fig. 149). The 'spiracles,' or 'stigmata' (*g*), through which air enters the tracheal system, are normally situated upon either side of each segment of the body; but they are often deficient in certain segments, those of the thorax especially. They differ

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* It is stated by Dr. T. Williams ("Ann. of Nat. Hist.," 2nd Ser., Vol. XIII., p. 193) that the minutest ramifications of the tracheæ are destitute of the spiral coil; with this statement the Author's own observations accord.

considerably as regards their complexity of structure; being sometimes mere slits, like button-holes; whilst in other instances they have two valves, which can be opened and shut (like the leaves of a folding-door) by muscular effort. They are frequently furnished, moreover, with a kind of sieve or grating, which filters-out the particles of dust, soot, &c., that would otherwise enter with the air, and soon block up the passages. The spiracles communicate by short wide canals (which sometimes exhibit vesicular dilatations that remind us of the sacculi of the Annelida) with the two long trunks (*f*), which pass from one end of the body to the other, and which give off branches whose ramifications extend through the body. The peculiar relation of these tracheal ramifications to the circulating system, has been already described (§ 226). The proportional size of the saccular dilatations, which are mostly formed on the principal trunks, varies greatly in different families. They are usually most developed in those that sustain the longest and most powerful flight (such as the Bee tribe), which are generally those whose larva-condition has been most imperfect, and in which there has been originally no appearance of these enlargements; on the other hand, they are almost entirely absent in the Insects destined to live upon the ground, or in them are little larger than the slight expansions found in the early conditions of such as undergo no complete metamorphosis. There can be little doubt that one use of these cavities is to diminish the specific gravity of the Insect, and thus to render it more buoyant in the atmosphere; but it would not seem improbable that they are intended to contain a store of air for its use while on the wing, as a part of the spiracles are at that time closed, so that less can enter from without.

303. The interchange of the air contained within this system of tracheæ and air-sacs, is accomplished by the alternate contraction and enlargement of the abdominal portion of the body. The abdominal segments are seldom covered by complete inflexible rings; for between the dorsal and the ventral half of each ring, a membranous portion usually intervenes; and thus the capacity of each segment may be diminished by the approximation of these two portions of its dense envelope, which is effected by muscular contraction. But the rings are also capable of being in some degree drawn-up one into another, like the sliding joints of a telescope; and in this way the abdomen is shortened as well as compressed vertically, so that a large part of the air contained in the tracheal system will be expelled from it. The enlargement of the abdomen, and the re-filling of the tracheal system, appear to be chiefly due (like the inspiratory movement of Birds, § 311) to the elasticity of all the parts that have been previously compressed, and probably in no small degree to the resiliency of the spiral fibre of the tracheæ.—These provisions are so effectual, that the amount of the aerating changes performed by an Insect in a state of activity, is not less in proportion to its bulk, than that effected by the most energetic of the Vertebrata (§ 322). It is impossible to view this subject philosophically, without being struck by the fact, that this very high degree of respiratory power is given, not by a sudden advance to a more complicated and perfect system of organs, such as exists in the Vertebrated classes of animals, but by an extension of the comparatively simple plan of which we observed the first traces in the Annelida; thus affording a

beautiful example of the great law of regular progression in the development of organs, which has few apparent and perhaps no real exceptions. Nor would it be easy for any reflecting mind to contemplate the manner in which the air is thus brought into contact with the blood in the minutest textures of the body, without a feeling of admiration at the contrivance shown in the compensation of the limited circulation of the fluids by the extensive distribution of the respiratory apparatus; and at the means by which the necessary lightness, elasticity, buoyancy, and muscular energy are imparted to the bodies of these beautiful and interesting inhabitants of the air.

304. In the *Larva* condition of such aerial Insects as undergo a complete metamorphosis, and are therefore most different in their early state from their ultimate character, the structure of the respiratory system closely corresponds with the type it had attained in the higher Myriapoda. We find it entirely consisting of ramifying *tracheæ*, connected with the external air by the spiracles that open on either side of the ventral surface of the body; and freely communicating with each other, especially by the two longitudinal tubes which traverse its length, and into which the stigmata open by short straight passages. Just as the *Larva* is passing into the *Pupa* state, the larger tracheæ exhibit dilatations at intervals, which are subsequently developed into expanded sacs that sometimes attain considerable size. The efforts which the animal makes at the moment of transformation, to rupture its skin by the distension of its body, appear to contribute towards the expansion of these sacs, the formation of which had previously commenced.* One remarkable portion of the tracheal system, also, the incipient evolution of which may be detected in the Larva state, now shows an increased tendency to prolongation;—that, namely, which forms the wings. It has been regarded as absurd to maintain that the wings of Insects are essentially a part of the respiratory apparatus; but that such is their real homology, is shown alike by their perfect structure, and by the history of their development. A very little examination into the structure of the *wings* makes it clear, that it is essentially the same as that of the expanded *branchiæ* of aquatic larvæ; each consisting of a prolongation of the superficial covering of the body over a system of ramifying 'nerves' or ribs, which are principally composed of tracheæ in connection with those of the interior of the fabric. During the first metamorphosis of the *Sphinx ligustri*, as observed by Mr. Newport, the wings, which, at the moment of slipping off the larva-skin, were scarcely as large as hemp-seeds, have their tracheæ distended with air; and, at each inspiration of the insect, are gradually prolonged over the trunk, by the propulsion of the circulating fluid into them. The enlargement of the tracheæ may also be observed in the antennæ, which just before the change were coiled-up within the sides of the head, but are now extended along the sides and abdomen. The complete development of the respiratory apparatus only takes place, however, at the time of the last metamorphosis; when the wings become fully distended with air, and prepared for flight by the active respiratory movements of the body; and the expansion of the pulmonary sacs then proceeds to a greater extent. It may frequently be noticed that, for

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* Newport 'On the Respiration in Insects,' in "Philos. Trans.," 1836.

some hours or even days after the perfect Insect has emerged from the pupa state, it makes no effort to fly, but remains in almost the same torpid condition with that it has quitted; when stimulated to move, however, it makes a few deep inspirations, its wings rapidly become fully expanded, and it soon trusts itself in the element which was intended for its habitation.

305. The various provisions which are made for the respiration of such Insects as inhabit the water, are of a nature too interesting to be passed-by. In those aquatic Larvæ which breathe air, we often find the last segment of the abdomen prolonged into a tube, the mouth of which remains at the surface while the body is immersed. The larva of the gnat may often be seen breathing in this manner, which calls to mind the elephant's elevation of his trunk when he is crossing rivers that entirely conceal his head and body. Sometimes this air-tube, which is to be regarded as a prolonged spiracle, is several inches in length, and its mouth is furnished with a fringe of *setæ* (or bristles), which entangle bubbles of air sufficient to maintain respiration when the animal descends entirely to the bottom; and the large tracheæ proceeding from this tube convey the air through the body in the usual way. Most aquatic Larvæ which are unpossessed of such an air-tube, have their spiracles situated only at the posterior extremity of the body, and may be seen apparently hanging from the surface, whilst taking-in the necessary supply.—There are some Larvæ, however, more particularly adapted to aquatic respiration, by the development of the tracheal system externally into plates or tufts, which have been appropriately termed *aeriferous branchiæ;* their object being not so much to carry the circulating fluid into contact with the water, as to absorb from that element the air it contains, which is then carried into the internal respiratory apparatus. Sometimes the membrane which covers the branchiæ, and which is a prolongation of the external surface, is continuous, so that the gills have a foliaceous appearance like that of the wings; but in other cases, it is divided, so that the branchiæ more resemble the filamentous tufts of the Nereis. Their position is constantly varying; sometimes they are attached to the thorax, sometimes to the abdomen, sometimes even situated within the intestine; but in most cases they have an important relation with the movements of the animal, and are frequently the sole organs of progression with which it is furnished. Thus the sudden darting motion of the larva of the *Libellula* (dragon-fly) is caused by the violent ejection, from the intestine, of the water which has been taken-in for the supply of the respiratory organs it contains; these consisting of a vast number of villous prolongations of the membrane lining the rectum, arranged in regular rows; each of which, instead of being supplied with blood-vessels, contains a minutely-ramified system of tracheæ communicating with the principal trunks. This appears to be the sole mode in which these larvæ obtain air; for their tracheal system has no external orifice, save a single pair of spiracles, which do not seem to give ingress or egress to air, except when the pupæ quit the water to undergo their last metamorphosis.* It is interesting to observe that this closed condition of the

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* See the interesting Memoir of M. Léon Dufour, 'Sur les Larves des Libellules,' in "Ann. des Sci. Nat.," 3^e Sér., Zool., Tom. XVII.

tracheal system seems to be a character common to other Insect-larvæ in an early stage of their development.*—All perfect Insects (with the exception of a Neuropterous insect, *Pteronarcys*, described by Mr. Newport as retaining its larval branchiæ in the Imago state) being adapted for tracheal respiration only, many curious contrivances may be witnessed among such as inhabit the water, for carrying-down a sufficient supply of oxygen to aerate their blood whilst they are beneath the surface. Some, for example, enclose a large bubble under their *elytra* (wing-cases), which, not being closely fitted to the exterior of the body, leave a cavity into which the spiracles open; whilst others have the whole inferior surface of the body covered with down, which entangles minute bubbles of air, in such large quantity as to render the insect quite buoyant, and to oblige it to descend by creeping along the stem of a plant, or by a strong muscular effort.

306. In the lower tribes of the *Arachnida*, such as the *Acaridæ*, the respiratory apparatus is usually constructed on the plan which prevails among Insects, being composed of a system of tracheæ, ramifying through the body, and opening externally by stigmata: this apparatus, however, would seem to be in some cases very imperfectly developed (§ 54). In the higher Arachnida, however, such as the *Spider*, *Scorpion*, &c., the circulating system is more complete, and there is no longer occasion for such universal aeration of the solid tissues, that of the nutrient fluid being sufficient. Accordingly the respiratory apparatus exists in a more concentrated state, which approximates nearly to that which has been described as possessed by the higher Crustacea; but, being adapted for aerial respiration only, it must be regarded as belonging rather to the pulmonary than to the branchial system. The spiracles or stigmata in these animals, usually four on each side, instead of opening into a prolonged set of ramifying and anastomosing tubes, enter at once into distinct sacs, disposed along the sides of the abdomen, to which the air has therefore ready access. The interior of these cavities is not smooth, however, like that of the pulmonary sacs of Insects, but is prolonged into a number of duplicatures or folds; these lie close to each other like the laminæ of gills, and may be regarded either as analogous to them, or as rudiments of the partition of the cavity into minute cells, like those of the lungs of higher animals. Each of these laminæ is described by Mr. Newport as consisting of an exceedingly delicate and apparently structureless double membrane, which includes within it a parenchymatous tissue formed of single cells aggregated together, their arrangement having a degree of regularity in some parts, but being quite irregular in others. The blood is brought to this organ by a vessel which runs round its convex margin; but it must be distributed over its surface by a lacunar circulation between the component vesicles of the parenchyma.†—Before quitting the Invertebrated classes, whose Respiratory apparatus, both atmospheric and branchial, has now been described, it is worthy of note that in no instance do their respiratory organs communicate with the mouth, which is an organ solely appropriated to the reception and subdivision of the food. It may also be remarked, that it is only in the

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* Dr. T. Williams in "Philos. Transact.," 1853, p. 639.

† "Philosophical Transactions," 1843, p. 296.

higher tribes that any muscular movements are performed, with express reference to the maintenance of the respiratory process by the renewal of the air or water which is required for it; this renewal, in the lower tribes, being accomplished by ciliary action, or by the general locomotive actions of the body.

307. We now pass on to the consideration of the Pulmonary apparatus of Vertebrated animals; a rudiment of which is found in most members of the Osseous division of the class of *Fishes*, notwithstanding that the aeration of their blood is otherwise provided-for. This rudiment is commonly known as the 'air-bladder;' which in many Fishes, as in the embryo of Mammalia, is a simple sac, placed along the middle of the back (Fig. 126, 10); whilst in others, its cavity is divided by one or more membranous partitions; and this division proceeds to such an extent in some instances, as to give to the organ the character of the lung of a Reptile. The air-bladder, in a large proportion of the Fishes which possess it, is closed on every side, its cavity having no connection with any other organ;* this is the case, for example, with that of the Perch, Cod, Mackerel, and other *Acanthopterygii* of Cuvier. But in most of the *Malacopterygii*, as the Herring, Salmon, Pike, Carp, Eel, &c., the air-bladder communicates with some part of the alimentary canal near the stomach, by means of a short wide canal termed the *ductus pneumaticus;* and in the *Cyprinidæ* (Carp tribe) this communication is formed with the œsophagus. The true relations of this organ are most remarkably shown in the *Lepidosteus* or 'bony-pike' of the North American lakes. This curious fish, which presents many Reptilian affinities, has the air-bladder divided into two sacs that possess a cellular structure; the trachea which proceeds from it opens high-up in the throat, and is surmounted with a glottis. Another fish may be mentioned as presenting an apparatus adapted for atmospheric respiration, which is rather a peculiar development of a portion of the branchial apparatus, than the rudiment of the lung of air-breathing Vertebrata; this is the *Cuchia*, the peculiarity of whose circulating system has been already noticed (§ 241). Here, as in the Synbranchus, there is but a single branchial orifice, which is situated under the throat; and this leads by a passage on each side to the gills, of which there are only two rows, and these but slightly developed. The principal organs of respiration are two vascular sacculi, prolonged from the branchial chamber, and placed on either side of the head; these communicate with the cavity of the mouth by two orifices, each of them provided with a sort of constrictor muscle which serves to contract or entirely close it, and which thus resembles a glottis; and into these, air is received for the oxygenation of the blood which is distributed upon their walls. From what has been said of the anatomical structure of this curious animal, it is obvious that it possesses the circulation of Reptiles, and the respiration partly of that class and partly of Fishes. Its blood will, therefore, be less oxygenated than in the regular types of either class; since the respiratory organs are less adapted for its aeration than are those of Reptiles, and only a part of the blood is sent to them, instead of the whole as in Fishes. To this deficiency we may attribute the

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* According to Von. Baer, the air-bladder is developed as a *process* or *diverticulum* from the upper part of the alimentary canal; so that, when it forms a closed sac, the original communication must have been obliterated. See *Note* to § 316.

obtuseness of its senses and sluggishness of its movements, which form a striking contrast to the vivacity of the Eel. It is generally found lurking in holes and crevices, on the muddy banks of marshes or slow-moving rivers. The power which the animal possesses of distending the respiratory sacs with air, while on land, and the necessity it is under of rising to the surface of the water for the same purpose, prove beyond a doubt that they perform the function of lungs; and lead us to the conclusion, therefore, that the Cuchia is 'amphibious' in the strict sense of the word—forming a connecting link between the Ophidian Reptiles and the Synbranchus among Fishes.*—In some other Fishes, especially such as naturally inhabit small collections of fresh water, whose temperature is liable to be considerably raised during the heat of summer, the mucous lining of the alimentary canal appears to serve as an additional organ of respiration; for such fishes are frequently seen to rise to the surface, and to *swallow* air, which is subsequently discharged by the anus, with a large quantity of carbonic acid substituted for its oxygen. This is the case, for example, with the *Cobitis* (loach); and it would seem as if, under these circumstances, some such supplemental means is required for carrying-on the respiratory process with unusual activity (§ 323).

308. It does not seem improbable that in those Fishes which possess a short and wide *ductus pneumaticus*, the air-bladder may serve as an accessory organ of respiration; atmospheric air being taken-in, and carbonic acid ejected, through the alimentary canal, in the manner just described. But in those whose air-bladder is a closed sac, it seems evident that it cannot in any way conduce to the aeration of the blood; and this is one of the instances, of which many might be pointed-out both in the Vegetable and Animal kingdoms, wherein the rudimentary form of an organ, that attains its full development in other classes, is adapted to discharge some office quite different from that to which it is destined in its perfect state. The gas which the air-bladder contains, is composed of the same elements as atmospheric air, namely, oxygen, nitrogen, and carbonic acid; but these are mixed in proportions that are very liable to variation. It has been said that oxygen is deficient in the contents of the air-bladder of fresh-water fishes, and is predominant in that of fishes which inhabit considerable depths in the sea. This organ is altogether absent in fishes which are accustomed to remain at the bottom, and whose movements are slow, such as the *Pleuronectidæ*, or 'flat-fish;' whilst it is of large size in those remarkable for vehement and prolonged movements, especially in Flying-fish of various species. It is generally supposed that the possession of an air-bladder enables the fish to alter its specific gravity, by compressing the bag or permitting its distension; but experiment shows that, after the organ has been removed, a fish may still retain the power of raising or lowering itself in the water.—In many Fishes, especially such as have either no ductus pneumaticus, or a narrow one, the blood-vessels of the air-bladder are developed into vascular tufts, which are sometimes spread over its interior, but are more commonly aggregated into one mass, which is spoken-of as a 'vascular gland' or 'vaso-ganglion;' the use of this organ is altogether unknown.

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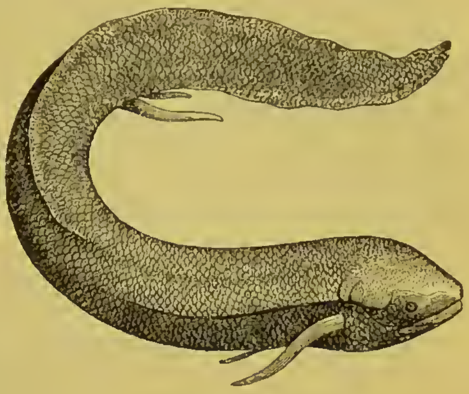
* Taylor, in "Brewster's Journal," 1831.

309. The members of the family of *Perennibranchiata* (which is the only true *amphibious* group) all possess lungs more or less developed; those of the *Proteus* being very similar to the air-bags of Fishes, whilst those of the *Lepidosiren* (Fig. 150) and of the *Siren* exhibit saccular depressions upon their internal surface, which are the first indications of a subdivision of the cavity into air-cells. The tube by which they open into the mouth bears a greater resemblance to the 'ductus pneumaticus' of Fishes, than to the trachea of higher animals; being simply membranous without an appearance of rings, while the glottis in which it terminates is a mere slit in the throat. Thus, the transition from the simple closed sac of Fishes, to the more complex subdivided lung of Frogs, is perceived to be very gradual; whilst, at the same time, the point of connection between the respiratory cavity and the alimentary tube may be observed to ascend, by similar gradations, from the stomach or some neighbouring part, to the œsophagus, and at last to the pharynx. Although all the animals which retain their gills, at the same time that they acquire lungs, are more or less adapted both to atmospheric and to aquatic respiration, the relative share taken by the two methods varies with the comparative development of their organs. Thus, in the *Siren*, the pulmonic respiration is more extensive and important than the branchial; but the reverse is the case in the *Proteus*. Even the Siren, however, dies, if its branchial respiration be prevented by desiccation of the gills. In the *Amphiuma* and *Menopoma* (whose early condition is not known) the lungs are more developed; and the animals seem to breathe by them alone, no branchial filaments being present.

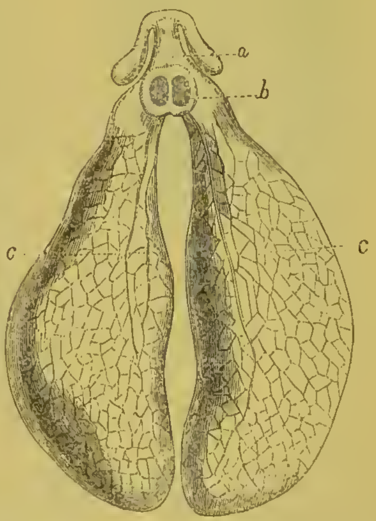
Fig. 150.



Lepidosiren paradoxa.

310. The lungs of the several orders of *Reptiles* are for the most part formed upon one type, being capacious sacs, the extent of whose vascular surface is but little augmented by sacculi developed in their walls: in the *Crocodilia* and *Chelonia*, however, there is an incipient subdivision of the principal cavity, which foreshadows, so to speak, that which is presented by the lungs of Birds and Mammals. The lungs of the *Frog* (Fig. 151) present a good illustration of the inferior type of pulmonated structure in

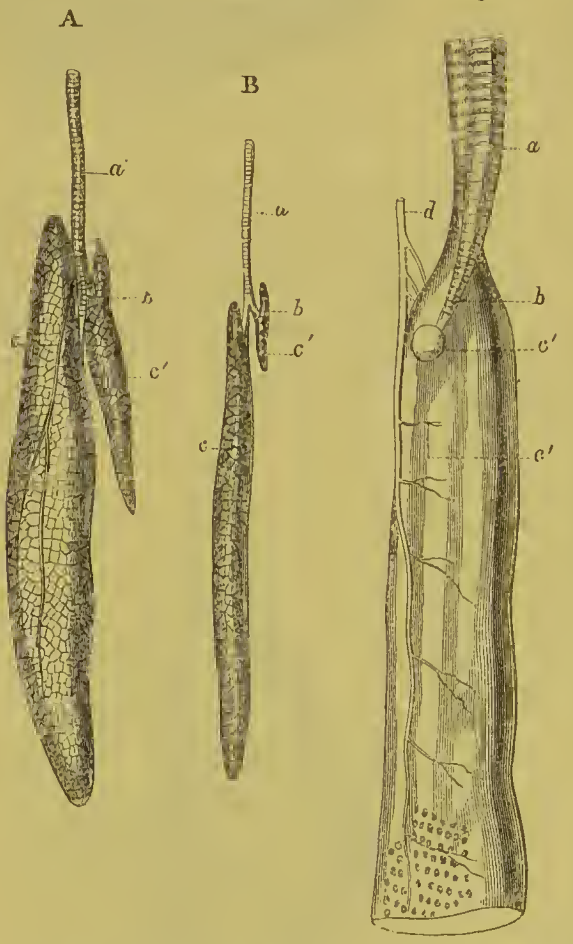
Fig. 151.



Respiratory organs of a *Frog*, as seen on their anterior surface:—*a*, hyoidean apparatus; *b*, cartilaginous ring at the root of the lungs; *c*, pulmonary sacs, covered with vascular ramifications.

the class of Reptiles. On laying them open, each is found to consist of a capacious cavity, in which the bronchus of its own side terminates, and on the walls of which the pulmonary vessels are distributed; these walls at the lower part are thin and membranous, but at the upper part they are strengthened by prolongations of the cartilaginous framework of the trachea, which forms a ring (b) at the root of the lungs; and these prolongations produce by their inosculation a cartilaginous network, in the interspaces of which are minute sacculi, whose lining membrane is crowded with blood-vessels. In this manner a set of 'air-cells' is formed in the upper wall of the lung, which communicates with the general cavity, and very much increases the extent of surface by which the blood comes into relation with the air introduced into the pulmonary organs; but each air-cell has its own capillary network on its walls, and consequently the blood is only exposed to the air on one side of that network, instead of on both as in Mammals (§ 313).—In *Serpents*, we usually find the pulmonary apparatus to consist of a single long cylindrical sac (Fig. 152, c), simply-membranous at its lower part, but furnished at its upper extremity with a cartilaginous reticulation projecting into its cavity, and inclosing in its interstices several layers of 'air-cells' with minutely vascular walls, which communicate through each other with the general cavity. The lung of the left side (c') is generally undeveloped. From the great capacity of their respiratory sac, the mobility of their ribs, and the power of their intercostal muscles, Serpents are capable of rapidly inspiring and expiring a large quantity of air, by which the want of an extensive surface is compensated, and energy is imparted to their muscular exertions. It is the prolonged expulsion of the air, after the lung has been fully inflated, that gives rise to the continued hissing sound by which these animals sometimes alarm their prey. In the aquatic serpents, the large body of air contained in the body serves to render it buoyant, and at the same time supplies the wants of the animal during a prolonged immersion.—In the *Saurian* Reptiles, we still find a very imperfect subdivision of the

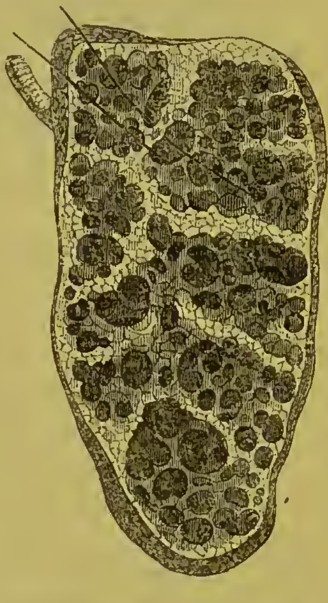
Fig. 152.



Lungs of the two sides, in A, *Bipes lepidopus*; in B, *Bimanus canaliculatus*; in C, *Coluber natrix*;—a, trachea; b, bronchial tubes; c, right lung; c', left lung; d, pulmonary artery.

pulmonary sacs; but they are equally developed on both sides of the body, excepting in those genera which approach the preceding order in the elongation of their bodies and the imperfect development of their limbs (§ 63); the left lung of these animals being either much shorter than the right (Fig. 152, A), or being almost undeveloped (B). In the lower forms of these organs, there is scarcely any appearance of sacculi, and they are usually much prolonged, frequently extending through the whole trunk, as in the Chameleon, as well as in many other Lizards; and their fulness or emptiness of air gives rise to the plump or lean appearance, either of which these animals have the power of assuming by the simple processes of inspiration or expiration. But when we have advanced upwards to the Crocodile, we find the lungs, though externally small, subdivided to a great degree of minuteness by internal partitions; and we also find the lungs more restricted to the thoracic region, with some indications even of a diaphragm, which is entirely wanting in all the inferior genera.* The structure of the lungs in Turtles and other *Chelonia* is very similar to that exhibited by the Crocodile tribe; the sacs have their cavities subdivided by incomplete partitions (Fig. 153); but they are still very capacious, and materially assist, by the quantity of air they contain, in buoying-up the heavy trunk of these animals when sailing on the surface of the water. —The relative inferiority of the respiratory apparatus of Reptiles is further shown in the absence of those means for effecting a continual interchange in the gaseous contents of the lungs, which we find in Birds, and still more in Mammals. In Batrachia and Amphibia, the lungs can only be filled with air by an action that resembles swallowing; and in Serpents and Lizards, although the movements of the ribs can in some degree effect such a compression and dilatation of the pulmonary cavity as shall occasion the egress and ingress of air, yet this is a slow and imperfect process compared with the rhythmical and efficient action of the diaphragm in Mammalia. Taken as a whole, this class is remarkable for the feebleness of its respiratory actions, and for the length of time during which the process can be suspended without injury. The demand for aeration is very much regulated, however, by the temperature to which the individual is subjected (§ 323).

FIG. 153.



Section of the Lung of the *Turtle*.

311. The respiratory apparatus of *Birds*, notwithstanding its extra-

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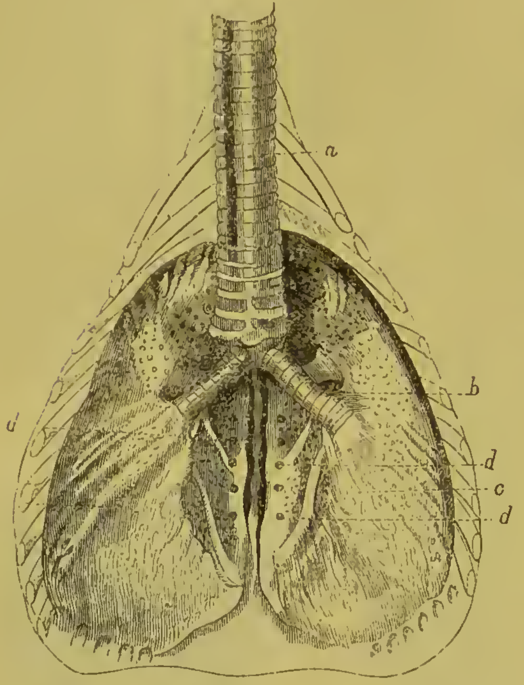
* Two openings are found near the cloaca of the Crocodile, leading from the external surface to the interior cavity of the abdomen, which is lined by the peritoneum; and it has been supposed by Geoff. St. Hilaire, that the superior energy of the Crocodile when immersed in water is due to the penetration of that fluid into the abdominal cavity, and the consequent conversion of the peritoneum into an additional respiratory surface. There is no sufficient reason, however, to believe that any such admission of water ever takes place, the canals being very small, and their orifices contracted; and it seems more probable that they are to be regarded simply as the remnants of the excretory ducts of the Wolffian bodies, of which traces are also to be found in the 'vaginal canals' of Ruminants and some other Mammalia.

ordinary extension, is intermediate, in its grade of development, between that of Reptiles and that of Mammalia; presenting, at the same time, features peculiarly its own. In this class, as in Insects, it extends through a great part of the body; large sacs connected with the lungs being contained in the abdomen, and even continued beyond the cavity of the trunk, as under the skin of the neck and extremities, where they seem to take the place of the ordinary 'bursæ mucosæ.'[*] These sacs freely communicate with the pleural and peritoneal cavities, of which they may in fact be regarded as extensions; and the pleural cavity communicates with the bronchial tubes by large open orifices that may be seen upon the surface of the lungs (Fig. 153*, *d*). Even the bones are made subservient to this function; for though at an early period they possess a spongy texture, like those of Reptiles, and are filled with thin marrow, they subsequently become hollow, and their cavities communicate with the lungs; in the aquatic species, however, the original condition is retained through life. In those Birds of which the bones are thus permeated by air, the trachea may be tied, and the animal will yet continue to respire by an opening made in the humerus or even in the femur. The minute structure of the lungs of Birds presents features of great

Fig. 153*.



Pulmonary apparatus of a *Pigeon*, as seen on removing the anterior wall of the thorax;—*a*, trachea; *b*, bronchi; *c*, lungs; *d*, apertures of communication with air-cells.

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[*] Various surmises have been formed as to the particular uses of these air-sacs in the economy of the Bird; and it does not seem improbable, that besides contributing to the function of Respiration by the extension of surface they afford, they have some subsidiary purposes. One of the most evident is that of rendering the body specifically lighter, as in Insects; and this will be obviously assisted by the great heat of the system, which rarifies the contained air. Again, the distension of the air-cells assists in keeping the wings outstretched, as is shown by the fact that inflation of those situated in the neighbourhood of their muscles is followed by their expansion; this must be a most important economy of muscular action, in birds which hover long in the air. Their evident analogy to the pulmonary sacs of Insects (§ 302) is confirmed by their relatively-larger dimensions in Birds of long-continued and rapid motion, than in the slow-moving tribes which are almost confined to the earth or waters. It has been remarked in addition, that "the same air which exerts its renovating influence upon the blood, supports all the more delicate structures which it reaches and surrounds, as a cushion of the most perfect softness and elasticity; so that by the most rapid motion, and the most violent twitches which the body receives in the changes and turnings of that motion, there can be no concussion of the parts more immediately necessary for the life of the birds." It would scarcely seem improbable that the large air-cells, which are found extending beneath the integument of the whole surface, especially the under side, of the Pelican and Gannet, serve to deaden the concussion which the body must experience, when the bird, after raising itself to considerable height in the air, lets itself suddenly fall upon the water in pursuit of its finny prey.

interest. The entire mass of each may be considered as subdivided into an immense number of 'lobules,' or 'lunglets,' each of which has its own bronchial tube (or subdivision of the windpipe), and its own system of vessels, which have but little communication with those of other lobules. Every lobule has a central cavity, which closely resembles that of the Frog in miniature, its walls being strengthened by a network of cartilage derived from the bronchial tube, in the interstices of which are openings leading to sacculi in their substance. But these sacculi are not, as in Reptiles, bounded by a distinct membrane, prolonged from that of the general cavity; for, with the exception of the part nearest the latter, the whole thickness of the wall may be considered as made-up of a very close plexus of blood-vessels, between the meshes of which the air penetrates freely without any limitation; and thus every capillary is in immediate relation with air on all sides,* a provision that is obviously very favourable to the complete and rapid aeration of the blood which it contains.—The lungs of Birds do not lie free in the thoracic cavity, like those of Mammals, but are bound-down on their dorsal aspect to its walls, as in many Reptiles; and their diaphragm is usually incomplete (its tendinous expansion losing itself on the bases of the lungs), so that the thoracic cavity is but imperfectly separated from the abdominal. The diaphragm is more complete, however, in the *Struthionidæ;* and in the *Apteryx* its conformation altogether resembles that of the diaphragm of Mammalia, though, as the air still passes into the pleural cavity, the mechanism of respiration must be less complete than in that class. From the elasticity of the bony framework by which the thoracico-abdominal cavity of Birds is surrounded, the state of fulness is natural to it, and that of emptiness is forced. The lungs and air-cells being full of air, they are partially emptied by the agency of muscles which draw the sternum nearer to the spinal column, and thus diminish the capacity of the visceral cavity; but when these muscles are no longer kept in contraction, the sternum springs outwards again, the cavity is restored to its original dimensions, and the air rushes-in to fill the lungs and air-cells. The distension of the lungs is further aided by the contraction of the diaphragm, which draws their bases downwards in the act of inspiration.

312. Of all animals, Birds are most dependent upon a constant renewal of the air in their lungs, and upon the purity of that with which they are supplied. Most Birds will die in air which has been but slightly charged with carbonic acid, and which can be respired by Mammals without immediate injury; whilst a greater degree of impurity, which is at once fatal to Mammals, can be sustained for a long period by Reptiles.—It is beautiful to observe that in Birds, as in Insects, the great extension of the respiratory surface is given by a simple increase in the capacity and prolongation of the sacs, and not by that concentration of it into a small bulk, which is effected by the minute partitioning of their cavity, and which indicates the highest form of the respiratory organs. Another analogy presented by their respiratory system to that of Insects, is this: In Insects the whole of the aeration is effected, by bringing the air into contact with the blood actually circulating through the system; whilst,

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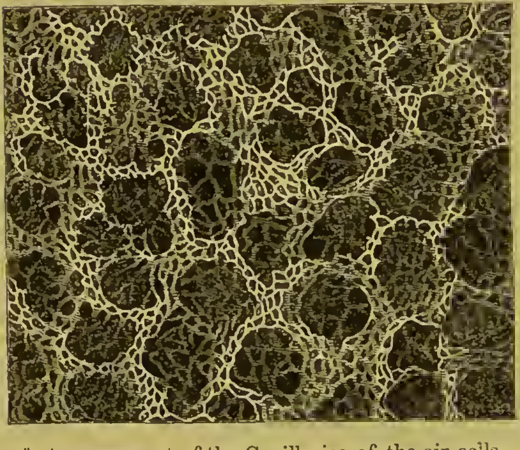
* See Mr. Rainey's description of the 'Minute Anatomy of the Lung of the Bird,' in the "Medico-Chirurgical Transactions" for 1849.

in the higher air-breathing animals, possessed of a more centralised apparatus (whether consisting of lungs or gills), the blood is transmitted through it by a special adaptation of the vascular system, in the intervals of its circulation through the body. In Birds we find a curious adaptation of the latter more elevated type to the Insect-like conditions of their existence; for, whilst the air introduced into the lungs acts upon the blood transmitted by the pulmonary vessels, that which fills the air-cells and cavities of the bones, comes into relation (as in Insects) with the capillaries of the system at large.

313. The respiration of *Mammalia* is not, like that of Birds, extended through the system, but is restricted to the lungs; and as a perfect diaphragm is now developed, which completely separates the thoracic from the abdominal cavity, these organs are confined to the former. Although their bulk is proportionally so much smaller than that of the pulmonary sacs of Reptiles, the actual amount of surface over which the blood is exposed to atmospheric influence is beyond comparison larger, owing to the very minute subdivision of their cavity. The want of capacity, too, is compensated by the active movements of inspiration and expiration, which constantly and most effectually renew their contents. The lungs are greatly developed in all the more powerful Mammalia, especially in the Carnivorous species; but they are comparatively smaller in their extent of surface, in the feeble and inferiorly-organised Herbivora; and the red corpuscles are much more numerous in the blood of the former, than in that of the latter. The varieties in the conformation of the lungs presented by the different orders of Mammals, relate chiefly to their exterior divisions, and to their greater or less capacity; the plan of structure being nearly the same in all. The whole interior of the lungs of Man and of Mammals generally, is divided into minute 'air-cells,' which freely communicate with each other, and with the ultimate ramifications of the bronchial tubes. The partitions between these cavities, the diameter of which in Man varies from 1-200th to 1-70th of an inch, are formed by double folds of basement-membrane, between which is a capillary plexus arranged in a single layer (Fig. 154); so that the blood in these capillaries is exposed to the air contained in the cells on *both* sides of it, but is not, as in Birds, brought into relation with the atmosphere without the intervention of a basement-membrane.* It has been calculated that the number of these air-cells grouped round the termination of each bronchial tube,

Fig. 154.



* Arrangement of the Capillaries of the air-cells of the *Human Lung*.

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* It is stated by Mr. Rainey (loc. cit.), that the lung of the Kangaroo, and even that of some Rodentia, presents a condition intermediate between that of Birds and that of the higher Mammalia; the air-cells, in the parts most remote from the surface, being very small, and being but imperfectly bounded by a basement-membrane.

—which cluster represents a 'lobule' of the lung of the Bird, and the entire lung of a Frog,—is not less than 18,000; and that the total number in the Human lungs is not less than *six hundred millions.* Some idea may be formed from this estimate, of the vast extent of surface which is thus provided, for bringing the blood into relation with the air.

314. This respiratory surface is brought into the most advantageous use possible, by the arrangements that are made for the continual renewal of the air which the lungs contain. The state of the thoracic cavity (which is always separated from the abdominal by the interposition of a complete diaphragm) that seems most natural to Mammals, is that of partial fulness; to empty it, and to fill it completely, alike require a considerable muscular exertion; but a moderate alteration of its capacity, such as takes place in ordinary respiration, is accomplished without sensible effort. Supposing the expiratory movement to have been just performed, the cavity of the chest, reduced to its smallest dimensions by the ascent of the diaphragm, the descent of the ribs, and the falling-in of the sternum, is enlarged in each direction by the contraction of the diaphragm, which diminishes the convexity of its arch, and by the elevation of the ribs, brings them more nearly into a straight line with their cartilages, and thus pushes forwards the sternum, whilst it separates the middle points of the opposite ribs from each other laterally, so as to increase the breadth of the cavity. A vacuum is thus created, which can only be filled by the expansion of the lungs; and they consequently become distended with atmospheric air, which rushes down the trachea, and makes its way through the ramifications of the bronchial tubes to the ultimate air-cells. When the inspiratory movement has been completed, the diaphragm relaxes and is pushed-up by the abdominal viscera, under the pressure of the abdominal muscles which are now called into contraction; whilst the ribs, no longer sustained by the contraction of their elevators, are drawn down again, partly by the contraction of another set of muscles, and partly by the elasticity of their own cartilages; so that the thoracic cavity is reduced in all its dimensions, and a portion of the air contained in the lungs is expelled from them—to be replaced by a fresh supply drawn-in by a repetition of the inspiratory movement.

315. From the preceding sketch of the progressive evolution of the Respiratory system in the animal scale, it will have been seen that the instrumental character of the respiratory organs is everywhere the same, however different their external form; and that it is only the disposition of their parts that is varied, in accordance with the circumstances in which their function is to be performed. The progressive specialisation of the function has been traced in ascending the series, by marking the evolution of a particular apparatus for its exercise, and the restriction of it to that apparatus; in no instance has any sudden change in character been witnessed, but, in the classes adjoining those in which a new organ was to be introduced, has been found some adumbration of it; yet even where the function is most highly specialised, the general surface is found to retain in some degree its participation in it. For the respiratory action is not confined to the lungs, even in animals which possess them in their most developed form. The blood which circulates through the capillaries of the skin is aerated by communication with the atmosphere,

wherever there is no impediment offered by the density of the tegumentary covering. In *Batrachia*, especially Frogs, the cutaneous respiration is of such importance to the animal, that, if impeded by covering the skin with oil or other unctuous substance, death will take place almost as soon as if the lungs were removed; and the animal may be supported for a considerable time by it alone, if the temperature be not too high (§ 277). In such circumstances, it is found that carbonic acid is generated in an atmosphere of hydrogen, as by pulmonary respiration. In like manner, if Birds or Mammalia be enclosed in vessels out of which their heads protrude, carbonic acid will be found to replace a portion of the oxygen; and a like result has been obtained by the similar enclosure of a limb of the Human body.

316. We shall now briefly trace the evolution of the Respiratory apparatus in the embryo of the higher Vertebrata; reserving, as before, the account of the earliest changes in the ovum to a future period (CHAP. XI.), and leaving until then the description of the organs which are peculiar to the fœtal condition, and which serve only to assist in the conversion of the nutriment that is supplied from the parent-system, as during the germination of seeds.—At about the third day of the development of the Chick, four pairs of clefts or transverse slits are observable behind the mouth, in the situation of the branchial apertures of Fishes; and at the same time, the branchial vessels are developed from the aorta, as already described (§ 256). One of the apertures is intermediate between each pair of vascular arches, just as in the gills of Fishes and Tadpoles. No branchial tufts, however, are developed; and the appearance described is very transitory, the vessels changing their direction and condition within two days. The development of perfect gills would have been useless, as the animal is not destined to be for a time an inhabitant of water like the tadpole, but has the aeration of its blood provided-for, until the time of the perfect evolution of its respiratory system, by an apparatus specially evolved for the purpose. The lung is developed, like the air-bladder of Fishes, as a *diverticulum* or process from the upper part of the alimentary canal. Soon after the middle of the third day, two minute wart-like projections are seen upon the tube, which are found to be hollow, and to communicate with its cavity.* These gradually increase in size; and the channels of communication become elongated into tubes. A little later, the tubes partly coalesce into one, and enter the pharynx by a single aperture. This is what we observe in the Proteus, and, as in that animal, the sacs are still simple undivided bags; after a little time, however, they send out prolongations in various parts, which again put forth others, so that the

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* The account in the text is given on the authority of Von Baer. Many subsequent observers, however, agree in stating, that the bud-like process in which the lungs originate, is not hollow but solid; being produced by a multiplication of cells of the external layer of the alimentary canal, into which its external tunic is not prolonged. According to this view, the downward extension of the cellular mass in which the lungs originate, is the consequence of the progressive multiplication of cells in that direction; whilst the production of the trachea and bronchial tubes is the consequence of the *fusion* of the cells in particular lines, as in the development of the great vessels. Viewed in this aspect, the absence of the 'ductus pneumaticus' in many Fishes is a result rather of non-development than of subsequent obliteration; and such would certainly seem to be by far the most probable account of it.

cavity becomes gradually more complex. The larynx and glottis are not perfectly formed until a late period.—The history of the evolution of these organs in Mammalia is precisely analogous. It is usually at about the sixth of the entire period of uterine gestation, that the outline of the branchial apparatus is seen, as marked by the shortness and thickness of the neck, by the penetration of the sides of the pharynx by the branchial clefts, and by the division of the aorta into vessels corresponding in number and distribution with the branchial arteries of fishes. These general features have been observed in the embryoes of most orders of Mammalia, not excepting Man himself; and they are probably common to all. A few days after the appearance of the fifth arch, which is the last developed, the neck begins to elongate, the apertures are closed gradually on the outside, while the vascular arches undergo those changes by which the permanent arterial trunks arising from the heart are formed (§§ 256—258). The lungs in Mammalia are developed much in the same manner as in Birds. They are not discernible before the period when the branchial apertures begin to close; a single mass is first perceived, which is soon divided into the rudiments of a right and left lung by a longitudinal groove; and the trachea and bronchi are subsequently developed, as in Birds.

317. Scarcely a more beautiful illustration could be adduced, of that Unity of Design which is manifested in the creation of different classes of animals, than this hidden but not obscured correspondence. Nor is the analogy confined to Animals alone; for it is impossible to compare the stages of the evolution of the perfect respiratory apparatus in the higher forms of the two kingdoms, without being struck with their essential correspondence. In the Flowering-plant we have seen a temporary respiratory organ, the *cotyledon*, first developed, like the branchiæ of a tadpole; and disappearing altogether, when the evolution of the permanent aerating apparatus renders it unnecessary. And just as the system which is the permanent one of the lower tribes of animals, is transiently indicated in the early development of the higher, so will it hereafter be shown (CHAP. XI.) that the foliaceous expansions of the inferior stemless Cryptogamia are to be regarded as the homologues of the cotyledons of Flowering-plants, which continue, in the inferior tribes, to perform their functions during the whole of life, like the gills of aquatic animals. That which has been said of the correspondence of the essential structure of the Respiratory apparatus, through all its varieties of external form, will apply with equal truth to its function also; for, in whatever tribe of Animals the changes composing it have been investigated, they are found to be of a very uniform character. The object of these changes appears to be, in all instances, the liberation of carbonic acid from the blood, the replacement of it by oxygen, and the exchange of nitrogen on one side or the other. It will be more convenient to enquire into the particular character of these changes, in the distinct form in which they are presented to us in the higher Animals, before proceeding to investigate their more obscure manifestations in the inferior tribes. These changes may be examined, either in the circulating blood, or in the air to which it has been exposed.

318. The most obvious difference between the Blood brought to the lungs for aeration after passing through the capillaries of the system, and

that which has undergone the process—or, in short, between 'venous' and 'arterial' blood—is its colour, which is dark purple (sometimes called black) in the former, and bright red in the latter. The alteration in colour may be produced by agitating venous blood with oxygen, or even by exposing it for a time to the atmosphere; in the latter case, however, only the surface acquires the arterial tint. The bright scarlet colour may also be given by the admixture of neutral salts; whilst the addition of acids renders it still darker, and prevents the change. It has been supposed until recently, that these effects are due to a chemical change produced by these agents in the hæmatine of the red corpuscles. But such would not appear to be the case; for when the hæmatine has been separated and diffused through water, it is neither darkened by carbonic acid, nor brightened by oxygen, unless some corpuscles be floating in the solution. Moreover, it is found that the action even of distilled water will darken an arterial clot. Taking all these circumstances in connection with the facts experimentally ascertained, in regard to the changes of form to which the red corpuscles are liable from the influence of reagents, it appears probable that the immediate effect of oxygen, like that of saline solutions, is to contract the corpuscles and thicken their walls, and thus, by altering their mode of reflecting light, to make them appear bright red; whilst carbonic acid, like water, may be seen to occasion a dilatation of the corpuscle, and a thinning of its walls (which are at last dissolved by it), in a degree that may be well supposed to produce the darkening of the mass formed by the aggregation.*—In what state of combination these gases exist in the blood, or whether they are present in a state of simple solution, has not yet been clearly determined. When venous blood is placed under the vacuum of an air-pump, a small quantity of carbonic acid gas is given out; but a larger amount, sometimes one-sixth of the whole volume, is evolved when the blood is agitated with atmospheric air, hydrogen, or nitrogen. Gas may be extracted also from arterial blood, by means of an air-pump capable of producing a very complete vacuum; and this is found to consist of a larger proportion of oxygen. From the experiments of Magnus, the latest and most satisfactory on the subject, it appears that the Oxygen in arterial blood amounts to about one-half of the quantity of Carbonic acid which it contains, but that in venous blood it is only about one-fifth; for whilst about 10 per cent. of oxygen, and 20 per cent. of carbonic acid, may be extracted from *arterial* blood, the quantity of oxygen removable from *venous* blood is diminished to 5, whilst that of carbonic acid is increased to 25. The relative quantity of Nitrogen is extremely variable.

319. The changes in the Air which has been respired, are capable of being examined with greater accuracy. They may be considered under four heads:—1. The disappearance of Oxygen, which is absorbed. 2. The presence of Carbonic acid, which has been exhaled. 3. The absorption of Nitrogen. 4. The exhalation of Nitrogen.—It was formerly supposed that the Oxygen which disappears, is the precise equivalent of the Carbonic acid which is generated, the latter gas containing its own bulk of the former. But it is now known that the amount of Oxygen which dis-

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* For a full discussion of this subject, see Scherer's Reports in the recent volumes of "Canstatt's Jahresberichte," and the works and memoirs to which he refers.

appears, is usually more than that which is contained in the Carbonic acid expelled, so that the surplus must be actually absorbed into the system. The amount of this surplus varies in such proportion, that it sometimes exceeds the third part of the carbonic acid formed, and is sometimes so small that it may be disregarded,—the difference depending, not only on the constitution of the species, but on the comparative degree of development, and more especially on the nature of the diet. This last fact has been established by the very careful experiments of MM. Regnault and Reiset,* who have shown that if the same animals be fed at one time upon flesh, and at another upon farinaceous food, the quantity of oxygen which is absorbed into the system is much greater in the former case, than in the latter. Thus it would seem evident, that the demand for oxygen in the system is partly connected with the metamorphoses which the alimentary materials undergo, in their passage through the body. Of the nature of these metamorphoses, our information is still very imperfect. —There is now quite sufficient evidence to prove that the generation of carbonic acid is not wholly due, as was formerly supposed, to the union of carbonaceous matter brought by the blood, with the atmospheric oxygen introduced into the lungs; since carbonic acid is not only found to exist in venous blood, but in the products of the respiration of gases entirely free from admixture with oxygen. Such an experiment can only be performed on animals, which can sustain for a time the absence of the stimulus of oxygen. That Snails confined in hydrogen will generate carbonic acid, was long ago shown by Spallanzani; but the later experiments of Edwards, Müller, &c. upon Frogs are more satisfactory, both from their superior accuracy, and from their freedom from the objection which might be raised against the others, on the ground of the low place of their subjects in the animal scale. It appears that, when confined in hydrogen, frogs will give out carbonic acid, for a time at least, as rapidly as in atmospheric air; and that the quantity generated in nitrogen is not much inferior. These results are evidently conformable to the principles formerly stated (§ 266) as regulating the mutual diffusion of gases. Owing to its energetic reaction with carbonic acid (occasioned by its great difference in specific gravity), hydrogen removes it from the blood with greater force than any other gas; so that venous blood will give off carbonic acid when exposed to an atmosphere of hydrogen, even after it has been submitted to the exhausting power of a vacuum. It is obvious, however, that, for the continued generation of carbonic acid, oxygen must be supplied from without, as there is no superfluity of it in the system.—The following, therefore, appears to be the history of the changes which the blood ordinarily undergoes in its passage through the body. In the capillaries of the lungs it becomes charged with oxygen, which it carries into those of the system; in the course of the actions which there occur between the nutritious fluid and the textures it supports and stimulates, part of the oxygen disappears, and carbonic acid takes its place; the venous blood, therefore, returns to the lungs, holding this in solution, together with the unabsorbed oxygen; and, in the capillaries of the lungs, the former gas is removed by the atmosphere, and replaced again by oxygen,—the interchange being entirely in accordance with the physical principles already stated.* From recent researches, however, it would seem that this is not the whole truth; for the elimination of the liver-sugar† (which may be constantly detected in the blood of the hepatic vein, of the vena cava, and of the pulmonary artery,) during the passage of the blood through the pulmonary capillaries (no sugar being ordinarily discoverable in the blood of the pulmonary vein or in that of the systemic arteries), seems to show that a combustive process must take place to a certain extent in the lungs themselves, as was long ago supposed.

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* "Annales de Chimie," 1849.

320. With regard to the absorption and exhalation of Nitrogen, it appears probable that both these processes are constantly going-on, but that their relative activity varies in different species, at different parts of the year, and under different circumstances. It appeared from the experiments of Dr. Edwards, that an increase in the volume of nitrogen in the respired air takes place in most young animals, and during the summer months; but that, in the autumn and winter, there is a considerable absorption when adult animals are employed. According to the recent experiments of MM. Regnault and Reiset (op. cit.), the exhalation of nitrogen is more common than its absorption; since warm-blooded animals in general, when subjected to their ordinary regimen, increase the amount of nitrogen in the atmosphere, in the proportion of from 1 to 2 per cent. of the oxygen consumed. But when food is withheld, or animals are fed upon a diet to which they are unaccustomed, an absorption of nitrogen takes place; and this was found to occur to a considerable extent in hybernating Mammals, whose production of carbonic acid does not go-on at more than 1-50th of the ordinary rate; so that their absorption of oxygen and nitrogen even exceeds the loss of carbon and that sustained by perspiration, and the animal actually increases in weight, without taking food, until it voids its excretions.

321. Animals whose respiration is aquatic do not decompose the water they breathe, but merely abstract the oxygen from the air contained in it; for if one of this class be placed in a limited quantity of water, from which it speedily exhausts the air, or in water from which the air has been expelled by boiling, it dies almost as soon as would an animal whose respiration is aerial, when placed in a vacuum. If, however, the surface of the water be in contact with the atmosphere, it will absorb air from it; and the life of the animal will be longer, the more fully the quantity thus obtained compensates for that which is consumed. When a Fish, in a limited quantity of aerated water, has reduced the proportion of air until its respiration has become difficult, it rises to the surface, and takes-in air from the atmosphere; and, if prevented from doing so, it dies much

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* This view of the function of Respiration was given in a paper which the Author published in the "West of England Journal" in 1835, as that which best accorded with the facts then known. It has been fully confirmed by subsequent experiments, especially those of Magnus; and it is the one now generally received. Notwithstanding that the proportions between the oxygen absorbed and the carbonic acid exhaled are so inconstant, that they cannot be reconciled with the numerical ratio of 1174 of the former to 1000 of the latter, which would constantly prevail if the force of 'mutual diffusion' were the only one that regulates the exchange, yet there seems to the Author no adequate reason for doubting that the process is mainly affected by the agency of that force; the minuter variations being determined by other conditions,—in part, not improbably, by the relative amount of the gases existing in the blood, and the tenacity with which it may hold them.

† The important discoveries of M. Cl. Bernard respecting the production of sugar in the liver will be noticed hereafter (§ 366).

sooner. The air thus taken-in probably acts upon the lining membrane of the intestines; for, after being expelled, it is found to contain a large proportion of carbonic acid.—The respiration of some of the inferior aquatic tribes, such as Crustacea, Mollusca, and Annelida, has been examined with similar results. According to the researches of Humboldt and Gay Lussac, the air contained in water is richer in oxygen than that of the atmosphere; the proportion being 32 per cent. in the former, and but 21 in the latter.

322. The respiration of Insects has been made the subject of accurate research by Mr. Newport;* and the results which he has obtained, correspond in a remarkable manner with those of Dr. Edwards's experiments on Vertebrated animals under different conditions. In those tribes which undergo a complete metamorphosis, the proportion of air consumed by the *larva* is much smaller than that which the perfect Insect requires, when their relative bulk is allowed-for, and their condition is the same as to rest or activity.† This fact is evidently analogous to one ascertained by Dr. Edwards, that in the higher animals, a greater quantity of oxygen is required in the adult state, in proportion to the size of the respiratory apparatus, than in the infant condition. Again, many larvæ can support a degree of privation of oxygen, which would be fatal to the perfect Insect; thus, there are some which inhabit the bodies of other insects, or are buried deeply in the soil, or seek their subsistence in noxious and unaerated places, all of which situations would be soon destructive to life in their advanced condition. This, too, finds its parallel in the history of the Vertebrated classes; for Dr. Edwards found that puppies, soon after birth, will recover after submersion in water for 54 minutes, thus bearing the privation of oxygen much better than the adult animal. The amount of respiration in the perfect Insect depends chiefly upon its state of activity or excitement. When its movements are rapid and forcible, the aeration of the tissues must be performed to a greater extent than when it is at rest; and the difference is manifested, as well by the respiratory motions, as by the amount of oxygen consumed. Thus the number of respirations in an Humble Bee (*Bombus terrestris*), while in a state of excitement soon after its capture, was from 110 to 120 in a minute; after the lapse of an hour they had sunk to 58, and subsequently to 46. Moreover a specimen of the same insect, confined in a limited quantity of air, produced in one hour after its capture, whilst still in a state of great activity, about 1-3rd of a cubic inch of carbonic acid; yet during the whole twenty-four hours of the succeeding day, the animal evolved a quantity absolutely less. The amount of respiration in the Pupa state is much less than in any other condition of the insect, which will readily be understood when its complete inactivity is remembered; the state of the animal at that time being comparable (so far as its respiration at least is concerned) to that of the hybernation of warm-blooded Vertebrata.

323. In *cold-blooded* animals in general, the activity of respiration is

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* "Philosophical Transactions," 1837.

† If a larva of the common Butterfly, for instance, has arrived at its full size at the time of making the observation, it appears to respire in a given time *more* than the perfect insect; but the result is liable to this fallacy—that the former is at least two-thirds larger than the latter, and is almost always in a state of activity, whilst the latter is frequently in a state of quiescence.

increased with elevation of the temperature of the surrounding medium. This has been shown in a very striking degree, with regard to the Amphibia, by the researches of Dr. Edwards; who found that when Frogs were confined in a very limited quantity of water, and were not permitted to come to the surface to breathe, the duration of their lives was inversely proportional to the degree of heat of the fluid. When it was cooled-down to the freezing point, the frogs immersed in it lived from 367 to 498 minutes; at the temperature of 50°, the duration of their lives was from 350 to 375 minutes; at 72°, from 90 to 35 minutes; at 90°, from 32 to 12 minutes; and at 108°, death was almost instantaneous. The prolongation of life at the lower temperatures is not due to torpidity; for the animals perform the functions of voluntary motion, and enjoy the use of their senses; but it is occasioned by the retardation of their rate of vital activity, which occasions a diminution of the demand for air, and a consequent postponement of the results of suspension of the supply. On the other hand, the elevation of temperature increases the demand for air, by augmenting the general activity, alike of the organic and of the animal functions; and thus renders the cessation of respiration more speedily fatal. The natural habits of these animals are in accordance with these facts; and the results of experiments on Fishes and on the hybernating Mammalia (which are reduced for a time to the state of cold-blooded animals) are to exactly the same effect. It is curious to observe that the degree of heat which obliges frogs to increase their respiration by quitting the water entirely, causes fishes to take-in air from the surface, as may be frequently witnessed during the summer, especially in small collections of water (§ 307). The amount of carbonic acid generated by Insects, also, increases with the surrounding temperature, other things being equal.—The activity of respiration in *warm-blooded* animals, on the other hand, is increased by a depression of the external temperature. Thus it was found by Letellier, that when small Birds and Mammals were enclosed in limited quantities of air, the quantity of carbonic acid produced in a given time was in close accordance with the difference between the temperature of the air and that of their bodies. The following were the amounts generated in an hour by the respective animals named, at the freezing-point, at a temperature near to that of their own bodies, and at an intermediate grade :—

	Temp. 86°—106°.	Temp. 59°—68°.	Temp. about 32°.
	Grammes.	*Grammes.*	*Grammes.*
A Canary	0·129	0·250	0·325
A Turtle-dove . .	0·366	0·684	0·974
Two Mice	0·268	0·498	0·531
A Guinea-pig . . .	1·453	2·080	3·006

Thus it would appear that the quantity of carbonic acid exhaled by Birds between 86° and 106° is not much more than *half* of that which is exhaled between 59° and 68°; and is only about *two-fifths* of that which is given-off at 32°. In Mammals, the quantity exhaled at 86°—106° is about half that which is given-off at 32°.—It is easy to understand the meaning of this difference in the effect of external temperature upon *warm* and *cold*-blooded animals, when viewed in its relations to their economy. For in the latter, the increase of respiration consequent upon the elevation of temperature is simply an exponent (so to speak) of the general vital activity of the animal, which heat tends to augment. But in the former, an elevation of external temperature decreases, whilst a depression increases, the demand for that internal combustive process, by which the standard heat of the body is maintained (CHAP. X., Sect. 3):

CHAPTER VII.

OF THE EXHALATION OF AQUEOUS VAPOUR.

1. *General Considerations.*

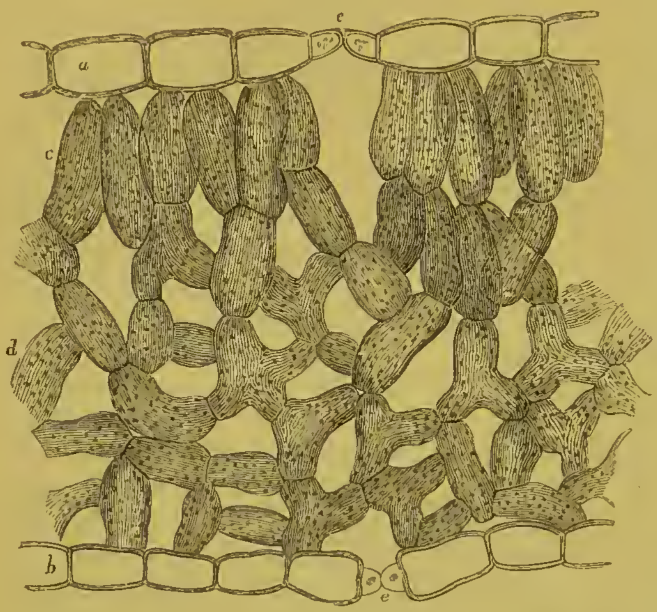
324. As all the alimentary materials taken into living bodies, for the nutrition of their solid tissues, are in a fluid form, being either dissolved or suspended in water, it is evident that a large quantity of that liquid must be superfluous, and that means must be provided for carrying it out of the system. This is partly accomplished, in Animals more especially, by its combination with various other ingredients,—which have either been introduced in greater quantity than the processes of nutrition require, or have already served their purpose in the vital economy,—into the *fluid excretions*, for the separation and deportation of which various arrangements are provided (CHAP. IX.) But besides the means thus afforded for the diminution of the superfluous fluid of the system, we find that the external surface has this function peculiarly imposed upon it, and that the disengagement of nearly pure aqueous vapour, though really the effect of simple evaporation, is principally dependent upon a special arrangement, by which its liberation from the circulating fluid is facilitated. This is most evident in Plants, where the quantity of fluid absorbed bears a much larger proportion to the amount of the solid matter contained in it, than it does in Animals; and where, from the little opportunity which there is for the introduction of superfluous nutriment, and the slight tendency to decomposition in the solid structures, the necessity for a constant excretion of other ingredients unfit to be retained is much less.

2. *Exhalation in Plants.*

325. The soft and succulent tissues of Vegetables, if freely exposed to the atmosphere, would soon lose so much of their fluid as to be incapable of performing their functions; and in all plants, therefore, which are subject to its influence, we find a provision for restraining such injurious desiccation. In the *Algæ*, however, and other tribes constantly immersed in water, or in a very moist atmosphere, no such loss can take place in their natural condition, and no means are required to prevent it. The outer layer of cells composing their integument, differs but little from those which it holds together, except in density; and it is accordingly found that such plants, when exposed to a dry air, speedily desiccate. All but the simplest Cellular plants, whose natural residence is the air, on the other hand, are covered with a membrane of peculiar character,

which is termed the *cuticle** (Fig. 155, *a*, *b*). This is composed of cellular tissue, the vesicles of which are flattened, and arranged with great regularity, in close contact with each other; and they differ from those of the parenchyma beneath, not only in form, but also in the nature of their contents. The form of these vesicles is different in almost every tribe of plants; thus in the cuticle of the *Iris* and of many other Monocotyledons, they are elongated, and possess straight walls and regular angles; whilst in that of the *Apple* and *Lily* (Fig. 156) their boundaries have a sinuous character. The cells of the cuticle are filled with a colourless fluid; and their walls are generally thickened by secondary deposit, especially on the side nearest the atmosphere; this deposit is usually of a waxy nature, and consequently renders the membrane very impermeable to liquids. In most European plants, the cuticle contains but a single row of cells, which are moreover thin-sided; whilst in the generality of tropical species, there exist two, three, or even four layers of thick-sided cells, as in the *Oleander*, the cuticle of which, when separated, has an almost leathery toughness. This difference in conformation is obviously adapted to their respective conditions of growth; since the cuticle of a plant indigenous to temperate climates would not afford a sufficient protection to the interior structure, against the rays of a tropical sun; whilst the diminished heat of this country would scarcely overcome the resistance afforded by the dense and non-conducting tegument of a species formed to exist in warmer latitudes.—Externally to this membrane, there usually exists a very delicate transparent pellicle, without any decided traces of organisation, though occasionally somewhat granular in appearance, and marked by lines which seem to be the impressions of the junction of the cells with which it was in contact. This membrane, the proper *epidermis*, is obviously formed by the agency of the cells of the cuticle; and is either a secretion from their exterior (as maintained by

Fig. 155.



Vertical Section of the Leaf of *Lilium album*; *a*, cells of the upper cuticle; *b*, cells of the under cuticle; *c*, *d*, cells of the parenchyma; *e e*, stomata.

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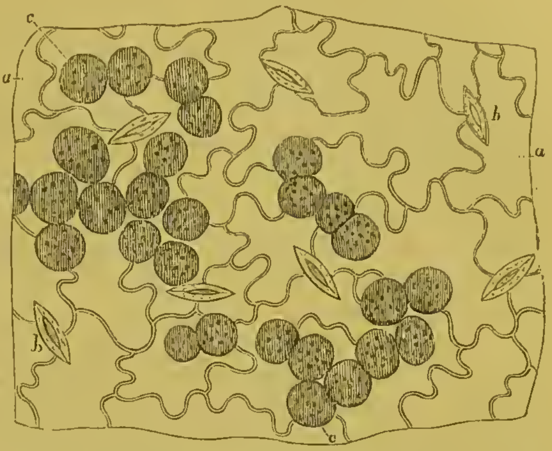
* Notwithstanding the usage of many distinguished Botanists, who apply the designation *epidermis* to this membrane, the Author has preferred retaining the term 'cuticle,' not only as being the one in common use in this country, but likewise as being the more appropriate. For by the term *epidermis* is implied, a membrane lying *upon* the dermis or skin; and therefore it can only be appropriately employed to designate the external pellicle presently to be described.

Schleiden, Payen, and others), analogous to that which forms a thick gelatinous layer on the surface of the Algæ, and which elsewhere constitutes the 'intercellular substance;' or itself consists of the external layers of the thickened walls of the cuticular cells, which have coalesced with each other, and which become detached from the subjacent layers by maceration (as affirmed by Mohl and Henfrey).

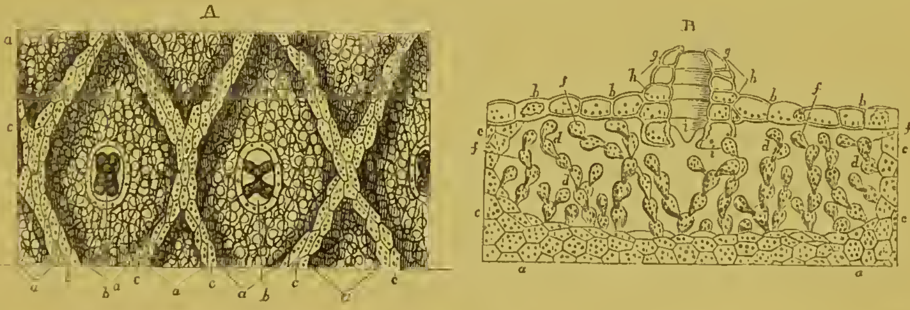
FIG. 156.



Under surface of the leaf of *Lilium album*; *a a*, cells of the cuticle; *b b*, stomata; *c c*, cells of the parenchyma in contact with the cuticle.

326. In the Cuticle of most Plants which possess such a structure distinctly formed, there exist minute openings termed *Stomata* (Fig. 155, *e*, *e*) which are bordered by cellules of a peculiar form, distinct from those of the cuticle, and more resembling in character those of the tissue beneath. These boundary-cells are usually in pairs, somewhat kidney-shaped (Fig. 156, *b*, *b*), with an oval opening between them; but, by an alteration in their form, the opening may be contracted or completely closed. They are sometimes more numerous, however, and the opening angular; and in the curious *Marchantia polymorpha*, their structure is extremely complicated. The openings in the cuticle of this plant (Fig. 157, A, *b*, *b*) are surrounded by five or six rings, placed one below the other, so as to form a kind of funnel or chimney, each ring being composed of four or five cellules (B, *h*). The lowest of these rings (*i*) appears to regulate the aperture, by the contraction or expansion of the cells which compose it. Wherever stomata exist in the cuticle, they are always found to open into cavities in the tissue beneath, which are thus brought into immediate

FIG. 157.



A, Portion of foliaceous expansion of *Marchantia polymorpha*, seen from above; *a a*, lozenge-shaped divisions; *b b*, stomata situated in the centre of the lozenges; *c c*, greenish bands separating the lozenges;—B, vertical section of the foliaceous expansion, showing *a a*, parenchymatous cellular tissue, forming the floor of the cavity; *b b*, superficial layer, covering-in the cavity; *c c*, cellular tissue forming the walls of the cavity; *d*, air-cavity partly occupied by loose cells *f f*; *g*, stoma divided perpendicularly; *h*, layers of cells forming its wall; *i*, cells forming the obturator-ring.

relation with the external air. In the Marchantia these chambers are very large, and are surrounded by regular walls (*c, c*); whilst in the leaves of higher plants they exist simply as intercellular spaces, left by the deficiency of the tissue. Stomata do not exist where there is no regular cuticle; and they are consequently not found upon the lower Cellular plants, and but very rarely on Mosses, in which group they seem to be restricted to the capsules or 'urns,' and to their 'setæ' or footstalks, on which parts the cuticle is more distinct from the subjacent tissue than it is elsewhere. They are not formed upon the cuticle of any plants growing in darkness, nor upon the roots, nor the ribs of leaves; but they exist in general on all foliaceous expansions, and on herbaceous stems, especially on those of which the surface performs the functions of leaves, as in the *Cacteæ*. They are most abundant on the under surface of leaves, except when these float on water, and then they are found on the upper side alone; but they exist equally on both surfaces of erect leaves, as in the Lily tribe and Grasses. It has been estimated that no fewer than 160,000 are contained in every square inch of the *under* surface of the leaves of *Hydrangea*, and of many other plants; and the greatest number seems to present itself in species, the *upper* surface of whose leaves is absolutely destitute of these organs. As a general fact, they are least abundant on succulent plants whose moisture is to be retained in the system; and they are frequently so imperfectly formed, as not to have any tendency to open, especially on the leaves of those adapted to exist in hot and dry situations. In all instances in which perforations exist, the tissue beneath is very loosely arranged, and contains many intercellular spaces; in the greater number of leaves, therefore, the most closely-packed cells will be found on the upper side (Fig. 155, *c*), whilst the parenchyma of the lower part (*d*) only comes into contact with the cuticle at intervals (Fig. 156, *c, c*); and it is to this arrangement, that the darker hue generally possessed by the superior surface, is principally due. If a leaf be placed in water, and the pressure of the air above be taken off, a number of minute globules will be seen to escape from these cavities, and to stud its exterior with brilliant points.

327. The loss of fluid from the surface of Plants may take place, as has been said, by ordinary *Evaporation*, or by proper Exhalation. The quantity of the former will be regulated by the degree of moisture in the tissue exposed to the atmosphere, and by the compactness of its arrangement. Thus, although the simpler terrestrial cellular plants, such as Lichens, have no true cuticle distinct from the subjacent tissue, their external layer of cells is generally of so dense a consistence, as to be almost impervious to water; so that their moisture is very slowly evaporated. The process is one quite independent of vitality, and is, indeed, the means by which dead plants are dried up, and by which the gradual loss of weight takes place from fruits, tubers, &c., that undergo no other alteration. It will, therefore, be influenced by those obvious external causes, under the control of which the process is universally performed; namely, variations in temperature, and in the humidity of the surrounding medium. —*Exhalation*, on the other hand, is a change which only continues during the life of the plant, and appears to be more closely connected with the performance of its other vital functions. If a piece of glass be held near

the upper surface of a vine-leaf in full growth in a hot-house, it is scarcely dimmed after some time; but if in proximity with the lower surface of the same leaf, it is speedily bedewed with moisture, which in a short time accumulates so as to form drops. This rapid transpiration of fluid appears to take place through the stomata, as it is now satisfactorily proved that it bears a strict relation (other things being equal) with the number of stomata on the plant, or on the particular part of it made the subject of examination. Various experiments have been made at different times, with the view of ascertaining the quantity of water thus transpired from different plants, and the circumstances most favourable to the process. With regard to *quantity*, the results obtained by Dr. Woodward* are among the most worthy of attention, although probably the earliest on record. Four plants of Spearmint were placed with their roots in water, and in a situation fully accessible to light, during 56 days (from June 2nd to July 28th); and the following table exhibits the quantity of water which each plant absorbed (proper allowance being made for the evaporation from the surface of the fluid), and its increase in weight at the end of the experiment. The *difference* must of course be the quantity exhaled, and would scarcely express the whole amount of it, as part of the increase in weight would be due to the fixation of carbon from the atmosphere.

	Original Weight.	Gain.	Water expended.	Difference.	
No. 1.	127 grs.	128 grs.	14,190 grs.	14,062 grs.	The water in which Nos. 3 and 4 were placed, had a little earth at the bottom.
No. 2.	110 grs.	139 grs.	13,140 grs.	13,001 grs.	
No. 3.	74 grs.	168 grs.	10,731 grs.	10,563 grs.	
No. 4.	92 grs.	284 grs.	14,950 grs.	14,666 grs.	
Total	403 grs.	719 grs.	53,011 grs.	52,292 grs.	

These experiments afford satisfactory evidence of the very large proportion of the absorbed fluid which is given out again by transpiration; and, joined with others by the same individual, they show that the activity of this function is much greater in summer than in the autumn.—A valuable series of experiments, communicated by Guettard to the Académie Royale in 1740, confirms this conclusion. He stated that transpiration is so much less active during the winter, than at other parts of the year, even in evergreens, that a Laurel parts with as much fluid in two days of summer, as during two months in winter. He also maintained that transpiration goes on much more rapidly under the influence of light and a moderate degree of heat, than at a high temperature but without light. —The experiments related by Hales in his essays on 'Vegetable Statics' will ever remain, like those which he performed on the Animal Circulation, a monument of his skill and perseverance. The results which he obtained from the accurate observation of a specimen of *Helianthus annuus* (Sun-flower) during 15 days, are those most frequently quoted by succeeding authors; but there are many others scarcely less interesting. This plant was 3½ feet high, weighed 3lbs., and the surface of its leaves was estimated at 5616 square inches. The mean transpiration during the whole period was found to be 20 oz. per day; but on one warm dry day it was as much as 30 oz. During a dry warm night, the plant lost 3 oz.; when the dew was sensible though slight, it neither lost nor gained; and by heavy rain or dew it gained 2 or 3 oz.—The following table shows the results of similar experiments on other plants.

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* "Philosophical Transactions," 1699.

Subject.	Surface.	Mean Transpiration.	Greatest Transpiration.	Depth.
Cabbage . .	2736 sq. in.	19 oz.	25 oz.	$\frac{1}{80}$
Vine . .	1820 sq. in.	$5\frac{1}{2}$ oz.	$6\frac{1}{2}$ oz.	$\frac{1}{191}$
Apple . .	1589 sq. in.	9 oz.	15 oz.	$\frac{1}{162}$
Lemon . .	2557 sq. in.	6 oz.	8 oz.	$\frac{1}{248}$
Plantain . .	2024 sq. in.	5 oz.	$11\frac{1}{2}$ oz.	$\frac{1}{112}$

The last column shows the mean quantity of water transpired from equal areas in the different plants (its depth being stated in parts of an inch) for the sake of ready comparison. That of the Sun-flower would be 1-165th; and is shown, therefore, to be less than half that of the Cabbage. The Lemon may be remarked to have exhaled far less than any of the others; and the same observation seems true with regard to evergreens in general.—An experiment performed by Bishop Watson will assist in giving an idea of the extraordinary amount of change effected by this function in Plants. He placed an inverted glass vessel, of the capacity of 20 cubic inches, on grass which had been cut during a very intense heat of the sun, and after many weeks had passed without rain; in two minutes it was filled with vapour, which trickled in drops down its sides. He collected these drops on a piece of muslin, which he carefully weighed; and, repeating the experiment for several days between twelve and three o'clock, he estimated, as the result of these inquiries, that an acre of grass land transpires in 24 hours not less than 6400 quarts of water. This is probably, however, an exaggerated statement; as the amount transpired during the period of the day in which the experiment was tried, is far greater than at any other.

328. The water exhaled is very nearly pure, so that what is furnished by different species varies but little in taste or odour. Duhamel remarked, however, that fluid thus obtained sooner becomes foul than ordinary water. Senebier analysed the liquid which he had collected from the exhalation of a vine at the commencement of the summer, and found that 40 oz. contained scarcely 2 grains of solid matter; and in a similar experiment on fluid collected at the end of the summer, 105 oz. gave but little more than 2 grains, or about 1-25000 part of solid matter. This minute impregnation does not indicate that any vital process of secretion is concerned in the process; since it is well known that the vapour of all water carries with it a small proportion of whatever substance the liquid may have held in solution.

329. All experiments point to the conclusion, that *Light* has a most important influence on the function of Exhalation. Thus it was shown by Senebier, that if Plants in which the process is being vigorously performed, be carried into a darkened room, the exhalation is immediately stopped; and that the absorption by the roots is checked almost as completely, as if the plant had been stripped of its leaves. Again, from the experiments of Dr. Daubeny,* it appears that exhalation is stimulated by the coloured rays of the solar spectrum in proportion to their *illuminating* not to their *heating* power, these two being separated by the prism; and Dr. D. further states that exhalation is not promoted by the most

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* "Philosophical Magazine," May, 1836.

intense degree of artificial light, in which he contradicts the opinion expressed by Decandolle. Still, it is certain that heat also, especially when combined with dryness of the atmosphere, has a greater effect upon the loss of fluid than light alone. It would not seem improbable, then, that the effect of Light is confined to the opening of the stomata, which it is believed to effect; and that the large quantity of fluid discharged from them, may be due to simple evaporation from the extensive surface of succulent and delicate tissue which is thus brought into relation with the air, and to the constant supply of fluid from within by which it is maintained in a moist condition.—If Plants are exposed to a light of too great intensity, especially if they are not at the same time well supplied with water, their tissue becomes dried-up by the increased exhalation which then takes place, and which is not sufficiently counterbalanced by absorption, so that their vegetation is materially checked;—a fact of which we see abundant evidence in dry sandy soils and exposed situations. If, on the contrary, the leaves are shaded, and the roots take up much moisture, the growth of the plant is active and luxuriant, but its tissue is soft;—an effect partly owing to the retention of fluid, and partly to the diminution of the quantity of carbon fixed from the atmosphere. If a plant be kept for some time in total darkness, so that it becomes *etiolated*, its texture is soft and succulent, and its tissue is distended with the moisture it has absorbed, and with which it cannot part; and if this state be allowed to continue too long, the leaves disarticulate and drop off, and the plant dies of dropsy. Succulent plants naturally require most light to secure for them a regular discharge of moisture; and there are some of this character which possess so few stomata, that they may be preserved out of the ground for many days and even weeks, without perishing from want of moisture. The thickness of their cuticle and their deficiency of stomata render it very difficult to dry them, even with the aid of heat; and it sometimes happens that *Sedums* and other such plants push considerable shoots, when placed under pressure whilst being prepared for the Herbarium.

330. The quantity of fluid lost by Exhalation, though ultimately dependent upon the degree of moisture supplied to the roots, does not appear to be increased by the propellent force of the sap; and this, observes the sagacious Hales, "holds true in animals, for the perspiration in them is not always greatest in the greatest force of the blood; but then often least of all, as in fevers." On the contrary, it is chiefly by the activity of Exhalation, that the amount of fluid absorbed is determined; just as the rate of ascent of oil in the wick of a lamp is dependent on the rapidity of combustion at its summit. Plants which exhale largely, therefore, must also absorb largely; and thus they are enabled to take-in and to appropriate, in considerable quantity, whatever nutrient materials the soil may contain. Such plants, moreover, have usually a great extent of green surface, by which they can obtain a large additional supply of carbon from the atmosphere; and thus their vegetative functions are performed with great activity, and they rapidly add to their growing parts. On the other hand, the plants which exhale slowly, absorb but little from the soil; and their fixation of carbon from the atmosphere is usually performed by a comparatively small surface, and at a comparatively slow rate; so that their whole vital activity is very

inferior, and the amount of solid tissue added to the fabric in a given time is far less. This is the case especially with succulent plants, whose soft and pulpy tissues are enclosed in a cuticle of peculiar density, that prevents the evaporation of their fluids; and whose life may be said to be remarkably slow. It is the case, also, to a certain degree, with most Evergreens; whose exhalation is slow, although their leaf-surface may be large, so that they fix a great quantity of carbon from the atmosphere; and it seems to be from this peculiarity, that their leaves possess a remarkable degree of firmness of texture, whilst they have a much longer duration of life than those of deciduous trees.—That by regulating the rate of Exhalation, through the influence of light and heat, we can affect the *rate of vital activity*, and consequently the *duration of life* (§ 336), appears from the well-known fact, that the freshness of a *bouquet* of flowers may be preserved for many days longer than usual, by keeping them in the dark.

3. *Exhalation in Animals.*

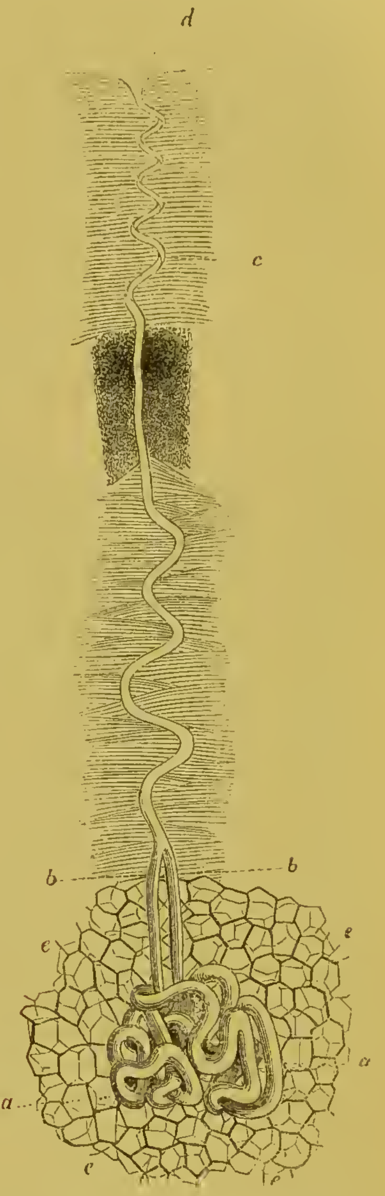
331. The loss of fluid which is constantly taking place from the surface of all Animals inhabiting the air, or at least from some part of it, appears due, like the exhalation of plants, partly to its physical, and partly to its vital conditions. There can be no doubt that from all soft moist surfaces, *evaporation* will take place in a warm and dry atmosphere; and the quantity of fluid lost in this manner will be in strict relation with the temperature of the surrounding medium, and the rapidity with which this medium passes over the evaporating surface. The process will of course be impeded by a humid state of the atmosphere, and entirely checked by contact of water, whether warm or cold, with the part which previously permitted it.—But there is another process by which fluid is exhaled from the surface, and which is more closely connected with the vital actions of the economy; this is the *transudation* from the blood, of a watery fluid, usually containing a small quantity of saline and animal matter in solution, through the instrumentality of a set of minute glands imbedded in the substance of the cutis or true skin. Each of these little bodies consists of a convoluted tube, in the neighbourhood of which the blood-vessels ramify minutely; this tube is continued to the surface of the skin as an excretory duct (Fig. 158), traversing the remaining thickness of the cutis and epidermis in a spiral manner, and opening by a very minute pore on the exterior of the latter, passing through it so obliquely that a kind of valve is formed by the membrane over its orifice. When the transudation of the sweat or 'sensible perspiration' is observed with a glass, as it occurs on the palms of the hands or the tips of the fingers, the first drop from each pore will be seen to be preceded by an elevation of this little valve. The ducts are visible in the form of delicate fibres passing from the cutis to the epidermis, when the latter is torn off.

332. The special object of the disengagement of fluid in the form of vapour, from the surface of the bodies of Animals, appears to be the reduction of the temperature. Animals which inhabit the water have no need of any special provision for keeping-down the temperature of their bodies within a certain limit; since the rapidly-conducting power of the medium is sufficient to reduce any superfluous amount of caloric which may be generated. The tenants of the deep, indeed, have very

little power of maintaining a temperature above it, unless they are provided, like the Whale tribe, with a layer of non-conducting fat, or, like diving Birds, with a downy covering possessed of a similar property. Moreover, the vicissitudes of temperature in large collections of water are never great, so that there is no demand from this source for a means of regulating the temperature of the individual inhabitants. But an Animal living upon the surface of the earth, exposed to constant and extensive atmospheric changes, and deprived of the power of rapidly parting with its heat, when superfluous, by mere contact with a conducting medium, has need of some special means, not only of generating caloric, but also of getting quit of it. The former will be hereafter described in detail (CHAP. X.); the latter is simply effected by the watery transudation from the surface, which, being poured-out of the perspiratory ducts in a fluid form, and carried-off as a vapour by the atmosphere, necessarily renders latent a large quantity of caloric, and thus diminishes the sensible heat of the exhaling body.

333. There is no evidence that either evaporation or transpiration takes place in *aquatic* animals; for whilst simple evaporation from their surface is of course prevented by the contact of water, the secretions which are formed in their integument would seem to be purely protective. When exposed to the air, all those which are formed of soft tissue, unprotected by a hard envelope, are rapidly desiccated, and usually perish; and it is evident that such Animals, when exposed to the atmosphere, are in the same condition with the Algæ among plants, which lose weight very rapidly, owing to the softness of their tissues and the want of a cuticle. Even amongst those which are provided with a hard envelope, there is always a peculiar tendency to evaporation from some part of the surface; thus, a very rapid evaporation of fluid takes place from the gills of the *Crustacea*, which would speedily offer a fatal impediment to the performance of their functions, if a special provision were not made for preserving their membrane in a humid condition (§ 293). From the experiments

FIG. 158.



Sudoriferous gland from the palm of the *Human hand*;—*a*, *a*, convoluted tubes, composing the gland, and forming two excretory ducts, *b b*, which unite into one spiral canal, that perforates the epidermis at *c*, and opens on its surface at *d*; the gland is embedded in fat-vesicles, which are seen at *e*, *e*.

of Dr. Edwards on *Fishes,* it appears that the loss of fluid by evaporation from the general surface of the body and from the gills, when the animal is exposed to the air, is so great as to be one of the chief causes of its death. Sometimes the impediment to respiration, which is produced by desiccation of the gills, is the immediate cause of death (§ 298); but where this is prevented, and the action of these organs continues during life, the surface parts with so much fluid by evaporation, that the body becomes stiff and dry, and previously to death loses from 1-14th to 1-15th part of its weight. Further, if the lower part only of the body be immersed in water, no absolute diminution in the weight of the whole takes place, and life is prolonged, although death at last results, seemingly from the unfavourable influence of dry air upon the branchial apparatus; but if, on the other hand, the head and gills be immersed and the trunk suspended in air, life may be almost indefinitely prolonged, although the drying of the surface of the part of the trunk exposed to the air is as marked, as in the case where these animals are entirely exposed to the atmosphere, and where they die after a considerable diminution in weight.

334. It is among *terrestrial* Animals, that the process of exhalation assumes a higher rank amongst the vital functions; and, even in the lowest classes, we find it exercising a very important influence on the condition of the system. Thus, in *Insects,* it has been ascertained by Mr. Newport, that the transpiration of fluid takes place to a considerable extent; and this not only in the species which have a soft external tegument, but among those which have the body encased in a dense horny envelope, such as the Beetle tribe. It is of course difficult to ascertain what proportion of the loss of fluid takes place, in each case, from the external surface, and from the prolongation of it that lines the air-passages, which in this class are so extensive and so minutely ramified; probably it is from the respiratory membrane, as in the Crustacea, that the principal liberation of it occurs. These observations show that Insects have the power of reducing their temperature, by this means, when it has been excessively raised by a continuance of rapid movements, or when the heat of the surrounding medium is too great.—It is among the *Batrachia,* however, that the exhalation of fluid from the surface is carried-on to the most remarkable degree, and seems to answer the most important purpose in the economy; and it is here, therefore, that its conditions may be most advantageously studied. Of the numerous experiments performed by Dr. Edwards on this subject, the following are the general results. He found that, when a Frog was placed in a dry calm atmosphere, the loss of weight during different succeeding hours varied considerably, but with a marked tendency to progressive diminution: that is to say, the more fluid the animal had lost, the less actively did exhalation go on. The actual quantity lost was influenced by various external agents, such as the rest or movement of the air, its temperature, and degree of humidity. Thus, frogs, hung in the draft of an open window, lost double, triple, or quadruple the amount exhaled by others placed at a closed window in the same room. The influence of the humidity of the air was tested by placing animals of the same kind in a glass vessel inverted over water; and it was ascertained that exhalation, if not then entirely prevented, was reduced to its minimum. On the other hand, when the dryness of the

air was maintained by quicklime during the progress of the experiment, the diminution of weight was found to be increased, the perspiration being from five to ten times greater in dry air than in extreme humidity, according to the duration of the experiment. The influence of temperature is shown principally in increasing the *transudation*, or Secretion from the skin; since the amount of fluid lost in a heated atmosphere differs but little, whether the medium be humid or dry, and increases in much more rapid proportion than mere evaporation would do. When Frogs were placed in an atmosphere saturated with humidity, by which mere evaporation would be almost or entirely suppressed, the loss by transudation between 32° and 50° was very slight, as also between 50° and 68°; but between 68° and 104° it was so great, that at the last-named degree its amount was 55 times that at 32°. The secretion is not even altogether suppressed by immersion in water. When Frogs are exhausted by excessive transpiration, and are placed in water, they speedily repair the loss by absorption from the surrounding fluid (§ 195); and the quantity thus gained sometimes amounts to *one-third* of their entire weight.

335. From his experiments on warm-blooded Animals, Dr. Edwards obtained results of a similar kind; but the influence of changes in external conditions was not quite so marked. The distinction between the simple *evaporation* which takes place in accordance with physical laws, and the *transudation* which is the result of a secreting process, must be kept in view, in order to account for their effects under different circumstances. It might, at first sight, appear to correspond with that between *insensible* or vaporous, and *sensible* or liquid transpiration; but this is not altogether true, since the *secretion* of the skin, if not very abundant, may pass off in the same form with the vapour which arises from its surface. The degree of *evaporation* from the skin of warm-blooded Vertebrata is modified, as in the Batrachia and other cold-blooded animals, simply by the temperature, degree of humidity, movement, or pressure of the surrounding medium. Wholly to suppress it, the air must not only be of extreme humidity, but must also have a temperature not inferior to that of the animal; since, if the air be colder, it will be warmed by contact with the body, and thus be capable of holding an additional quantity of aqueous vapour in solution. Although cold, therefore, diminishes or even altogether suppresses transudation, evaporation will continue to a certain extent. In Man, as in the Batrachia, it seems probable that *heat* alone stimulates the function of *secretion* from the skin; so that, at moderate temperatures and in ordinary states of the atmosphere, the quantity transuded is not more than one-sixth of that which is evaporated: whilst at an elevated temperature, especially if the air be already humid, the amount of secretion will much surpass that lost by evaporation; but if the air be dry and sufficiently agitated, evaporation may increase nearly in the same ratio.—Of the quantity of fluid which may be set free by exhalation within a short time, an idea may be formed from the observations of Dr. Southwood Smith upon labourers at the Phœnix Gas Works.* These men are employed twice a day in emptying and charging the retorts and making up the fires, for about an hour on each occasion; the labour is performed in

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* "Philosophy of Health," Vol. II., p. 322.

the open air, but is attended with much exposure to heat. On a foggy and calm day at the end of November, when the temperature of the external air was 39°, and the men continued at their work for an hour and a quarter, the greatest loss observed was 2 lb. 15 oz., and the average of eight men was 2 lb. 1 oz. On a bright clear day in the middle of the same month, when the temperature of the surrounding air was 60°, with much wind, the greatest loss was 4 lb. 3 oz., the average being 3 lb. 6 oz. And on a very bright and clear day in June, when the temperature of the external air was 60°, without much wind, the greatest loss (occurring in a man who had worked in a very hot place) was 5 lb. 2 oz., and the average of all was 2 lb. 8 oz.—From the experiments of Lavoisier and Seguin it appears, that the average amount of aqueous exhalation passing off insensibly from the human body is about 3½ lbs. daily; the maximum being 5 lbs., and the minimum 1¾ lb. Of this, however, a considerable proportion is set free from the pulmonary surface; the pulmonary being to the cutaneous exhalation, according to the estimate of Seguin, as 7 to 11. There is no reason to believe that the pulmonary exhalation is liberated in any other way than by *evaporation*, under the peculiarly favourable circumstances afforded by the delicacy and permeability of the respiratory membrane, its constant supply of fluid blood, and the frequent renewal of the air in contact with it. It is obvious that changes in the external conditions will have much less influence upon *its* amount, than upon the quantity evaporated from the skin; since the temperature of the air in the pulmonary cells must be nearly uniform under all circumstances (in the healthy state at least), and its movements are uninfluenced by the variations of the atmosphere. If, however, the external air be saturated with moisture, and be of the same temperature with the body (so as to be unable to acquire, by *its* heat, an increased capacity for vapour), it is obvious that the evaporation from the lungs, as well as that from the skin, will be entirely checked. This, indeed, appears to be the explanation of the peculiar feeling of oppression, which is consequent upon exposure to an atmosphere that is not only hot but moist. Under such circumstances, the temperature of the body is no longer kept-down to its proper standard by evaporation from its surface; and at the same time the capillary circulation of the skin and lungs is probably disturbed, by the obstruction to the elimination of fluid which should normally take place through these organs.

336. From the foregoing facts it would appear, that we may look upon the process of Exhalation as essentially *physical* in its character. That portion of it which consists in simple evaporation from the cutaneous surface, is obviously so; and as to that which is eliminated by the agency of the sudoriparous glandulæ, it seems probable that it also may arise from the mere exudation of the watery parts of the blood through their thin-walled capillaries. We shall hereafter see that the escape of the superfluous water of the blood through the Kidneys, may be looked-upon in precisely the same light (§ 421); and as we know that any medicinal agent which specially determines the blood towards those organs, will produce an augmentation in the watery portion of the urine, so does it seem probable that the stimulus of external Heat, which specially determines the blood to the Cutaneous vessels, would occasion an increased pressure from within, and consequently an augmented passage of fluid

through the walls of the capillaries. That the watery portion alone should pass, whilst the albuminous and saline matters are kept-back, can be easily comprehended, from the facts already cited (§ 168) in regard to the very low tendency to 'diffusion' exhibited by albumen, and the special power of retaining it which is possessed by animal membranes.

CHAPTER VIII.

OF NUTRITION.

1. *General Considerations.*

337. The function of *Nutrition* may be regarded as consisting of that series of changes in the Alimentary materials, by which they are converted into Organised tissues, and thereby acquire Vital properties. The new tissues thus generated may either constitute an *augmentation* of the previous fabric, as is the case with Plants even to the end of their lives, with the Zoophytic and other forms of Animals whose increase by gemmation is indeterminate, and with all Animals during their period of immaturity; or they may *be substituted for* tissues of an inferior order, without any necessary increase of bulk; or they may simply *replace*, by a similar production, the loss by disintegration, which the fabric at large, or any particular portion of it, may have undergone from the various causes formerly enumerated (§§ 112–114), in Animals which, having attained their full dimensions and complete organisation, exhibit no change in size, form, or intimate structure during long periods of time. In the first case, the Nutritive operation manifests itself in *Growth;* in the second, in *Development;* in the third, in *Maintenance:* in all cases, however, it appears to be essentially the same, and may be considered as the end and aim of all the other Organic functions, in so far as they are concerned in maintaining the life of the individual. For its continuance is dependent, in the first place, upon the *Absorption* of alimentary materials, and hence (in Animals), upon the preliminary process of *Digestion;* secondly, it requires the maintenance of the *Circulation*, for the transmission of the absorbed fluid, from the points where it is taken-in, to those at which it is to be applied; thirdly, it cannot long be carried-on without the continuance of *Respiration*, the vital properties of the fluids being only maintainable by free communication with the atmosphere; fourthly, it requires the separation of whatever is superfluous or injurious in the nutritive fluid, and thus becomes dependent on the due performance of the process of *Exhalation* in Plants, and on that of *Excretion* in Animals.

338. Every component part of each organism, as already shown, possesses an individual life of its own, whilst it contributes to support the Life of the entire being; this last being dependent upon the due performance of the vital actions of all its subordinate parts. But the degree of this dependence differs greatly in the different ranks of Organised beings; and thus the conditions under which the Nutritive function is performed, present a very remarkable diversity, which influences the apparent

character of the result, notwithstanding that the essential nature and tendency of the operation is the same in every case. Thus in the lowest forms of Organised beings, the entire fabric is made-up of repetitions of the same simple elements, and every part can perform its functions independently of the rest. In such, every act of nutrition is in fact an act of *growth;* for the tissues never advance beyond the simple cellular character which is common to every part of these homogeneous bodies; and it consists merely in the multiplication of cells by the act of subdivision (§ 22), each cell thus produced living for itself alone, and going through all its operations without influence or assistance from the rest. Precisely the same is the case with the early embryo of all the higher forms of organisation; for this, too, is composed of a homogeneous mass of cells (§ 73), increasing in number by subdivision, and having no dependence upon one another for the conditions of their vital activity. But as we ascend in the series, we find that the simple cellular tissues give place in greater or less degree to others, which are evolved out of them by a process of 'histological transformation;' thus from the simple Cellular Plants, we ascend to those in which woody fibre and various forms of ducts are combined with cells; and in the Animal series, we meet, very low in the scale, with fibrous and membranous, muscular and nervous, horny and calcified tissues, which depart more or less from the original cellular type. Here, then, the act of Nutrition does not consist in growth alone, but involves *development,* not merely in the first evolution of the organism from the embryonic state, but also in every change which it subsequently undergoes. And it is in proportion to the heterogeneousness of this development, as already shown, that the several parts of the organism become more and more dissimilar to each other in structure and function, and consequently more dependent upon one another for the conditions of their vital activity; so that at last the integrity of the whole structure, and the complete performance of its *entire series* of actions, comes to be necessary for the continual maintenance of any *one.* But notwithstanding that the life of the individual parts seems to be thus merged (so to speak) into that of the organism formed by their aggregation, it is so more in appearance than in reality; for although a bond of mutual dependence is created by the 'division of labour' which has been established in the organism, yet the integrity of each individual part remains as much dependent upon the due discharge of its own vital activity, as it is in those simpler forms of organic existence, in which every cell lives *for* and *by* itself alone.

339. As every component part of the most complex Organised fabric has an individual *life* of its own, so must each have a limited *duration* of its own, quite irrespective of the condition of the fabric at large, except in so far as this may tend to increase or diminish its functional activity. We find, however, that this duration varies greatly in the different kinds of organised tissue; and they may be classified in relation to this attribute, under the following heads:—

I. Cells may be generated, which have a very transient existence, and which die and disappear again without undergoing any higher development.—This is the case, for example, in the course of the formation of the pollen-grains, and at a certain stage of that of the ovule, of Flowering-Plants; in which the production of temporary cells, that afterwards liquefy again, appears to take place as a preparation for the formation of higher and more permanent structures. In Animals we have very numerous examples of the same general fact. The 'germinal vesicle' of the ovum seems to become filled with cells before its disappearance, and yet no trace of these cells can be afterwards detected; so that it would appear as if they too had deliquesced, leaving their component particles to perform some further part in the process of development. The various classes of Assimilating cells of which an account will be given in the present chapter, and the greater part of the Secreting cells (§ 401), appear, in like manner, to have a *very* transient existence, in the warm-blooded animal at least; their allotted functions being all performed within a few days or even hours, and their term of life being brought to a close as soon as this is the case.

II. There are certain component parts both of Vegetable and Animal organisms, whose duration is not less determinate, although it is more extended. This is the case, for example, with the reproductive organs of a large number of Plants (as the flowers of Phanerogamia, the urns of Mosses, and the pileus of Agarics), and with the capsules which seem to represent them in the Hydroid Zoophytes; for these parts are developed only to serve a particular purpose, which is speedily accomplished, and they then die and are cast off. So, again, the leaves of Plants, and the polypes of the compound Hydroida, which are the organs most actively concerned in preparing nutritive material for the permanent fabric, have a limited though longer duration; and in the higher Animals, we find a considerable number of structures which undergo a periodical exuviation, these being for the most part epithelial or epidermic in their character. Thus, in a considerable proportion of the Articulated tribes, the external integument is thrown-off many times during life, and is replaced by a new covering; a similar repeated moulting of the whole epidermis at once, takes place in Frogs, Serpents, and other Reptiles; in Birds, the feathers are thus periodically cast-off and renewed; in Mammalia, generally, the hair is regularly shed at certain parts of the year, whilst in Man there is a continual exuviation of the outer layers of the epidermis, and in the Deer tribe even the massive antlers are cast-off and renewed every year. Even the Teeth are limited in their duration among Reptiles and Fishes, being continually cast-out, to be renewed again; and a similar limit exists in the case of the deciduous or milk-teeth of Mammalia, which are shed at a determinate period of life.—Now in most of these cases, it is capable of being clearly proved that the *exuviation is consequent upon the death* of the component elements of the part thrown-off, not the death upon the exuviation. For with respect to the leaves of Plants, we have seen (§ 265) that they cease to perform their peculiar vital operations, and that the changes characteristic of decomposition commence, whilst they are still connected with the axis. So it has been pointed-out by Mr. Paget,* that the death of the hair-bulb precedes the falling-off of the hair; and it is a familiar observation that the absorption of the fang of the deciduous tooth, which could not take place without a previous degeneration, very commonly occurs before it is pressed-upon by the permanent tooth which is rising-up to occupy its place. So, also, it may be shown by acetic acid or potash, that the outer layers of epidermis are in a state of degeneration, for these reagents produce very little effect upon them, whilst they render the younger cells of the interior layers transparent, as they do other tissues in a state of active growth. The ova, too, as Mr. Paget remarks (Op. cit., p. 14), exhibit a remarkable fixity in their term of existence. "These attain their maturity in fixed successive periods of days; they are separated (as some of the materials of several other secretions are) while yet living, and with a marvellous capacity of development, if only they be impregnated during the few days of life that remain to them after separation; but if these days pass, and impregnation is not effected, they die, and are cast out, as impotent as the merest epithelium-cell."

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* "Lectures on Surgical Pathology," Vol. I., pp. 8—11.

III. In striking contrast with the limited duration of such parts, is the condition of those tissues, whose function, instead of being transient, is to be indefinitely prolonged; but such prolongation is seen only when the function, instead of being *vital*, is simply *physical*,—as in the case of parts that afford mechanical *support*, or resist *tension*, or supply *elasticity*. Thus, among Plants, mechanical support is afforded by the deposit of hard matter in the interior of the cells, tubes, &c., of which the part may be composed, as in the 'heart-wood' of the axis, the 'stones' of fruit, &c.; and the tissues so consolidated are cut-off from the general current of vital action. Among Animals, again, we meet with the same method of consolidation, by deposit within cells, in the shells of Mollusca and in the epidermic tissues of Vertebrata; whilst the shells of Echinodermata and the bones of Vertebrata appear to be formed rather by the chemical union of calcareous matter with a fibrous basis. When this consolidation has been once effected, the hard tissues, if not subjected to disintegrating agencies external to themselves,* may undergo little or no change for an almost indefinite period. Thus, the heart-wood of trees, the bones and shells of animals, and still more their hair, hoofs, horns, &c., may remain unaltered through an unlimited series of years. Of some of these parts it can scarcely be said that they are less alive, when removed from the organism to which they belonged, than when included in it. In the heart-wood of a Plant, for example, no vital change takes place, from the time that the woody tubes and fibres have been consolidated by internal deposit; it may decay, whilst still forming part of the stem, without the nutritive operations of the fabric being thereby interfered-with; and if we could possibly remove it entirely, without doing injury by the operation to the rest of the structure, its absence would be productive of no other evil consequences, than such as would result from the withdrawal of the mechanical support afforded by it. The same may be said of the stony 'corals' formed in the soft bodies of Zoophytes and Bryozoa, and of the dermal skeletons of Echinodermata and Mollusca; which remain unchanged, except by addition, from the time of their first formation, not only during the whole life of the animal to which they belong, but for an indefinite period after its termination. It is probable that the same would hold good, also, of the osseous skeleton of Vertebrata, if it were not for the necessity which exists for continually re-moulding this in accordance with the growth of the body, and for providing for its reparation when it has been injured after the attainment of its full dimensions.—The same indisposition to spontaneous change shows itself in the simple Fibrous tissues, which, after their first formation, seem to require but little maintenance, their chemical composition being such as indisposes them to spontaneous decay, and their functions in the economy being purely physical. Hence, when these tissues are generated by the transformation of cells, it seems as if these cells, in becoming converted into fibres, had almost entirely parted with the distinguishing attributes of vitality, and had thus passed into a condition in which no necessary limitation is imposed on their continued existence. And when developed simply by the fibrillation of a blastema, or by the coalescence or extension of nuclear particles, it seems equally true that the vital attributes of the matter in which they originate, cease with the conversion of that matter into the form of an organised tissue.

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* Thus the shells of many Mollusca are altered in form, not merely by the addition, but by the removal, of parts; this, however, seems to be effected by some *superficial* rather than by *interstitial* action, like that by which many Mollusca bore into rocks.

IV. The duration of the component tissues of the Nervo-Muscular apparatus, seems to depend mainly upon the degree in which their vital energies are called forth. When they are left in a state of inaction, they appear to partake, with other soft tissues, in the general attribute of limited duration; for we find that they undergo a gradual degeneration, and slowly waste away, the rate at which they do so being principally determined by the temperature. But when they are called into functional activity, it would seem as if the expenditure of their vital force put an *immediate* termination to their lives; so that their elements are at once resolved into inorganic compounds, by the oxygenating power of the blood. Hence we see that no rule can be laid down, as to the duration of the muscular and nervous tissues; since the exertion of their vital powers for no more than a few minutes, will occasion a larger amount of disintegration, than would otherwise occur during many weeks in warm-blooded animals, or during as many months or even years in the prolonged torpidity of cold-blooded animals or even of hybernating Mammalia.

340. It may be stated, then, as a general rule, applicable to all the foregoing cases, that the duration of an organised structure is very closely related to the activity of its vital manifestations; and that this, again, is related, on the one hand, to the character and attributes of the tissue, and on the other, to the conditions in which it is placed. Thus there are certain tissues (such as the Nervous substance of Animals), which would seem disposed to undergo very rapid change, in virtue alike of their chemical composition and of their vital endowments; whilst there are others (such as the Leaf-cells of Plants) whose component elements have not the same inherent tendency to separation, and the discharge of whose functions does not seem to involve the same immediate loss of vital power. But whilst the duration of the leaf-cells of a Plant may be reduced by unusual intensity of heat and light to a much shorter period than usual, the duration even of the nervous tissue of a cold-blooded Animal in a state of torpidity would seem to be protracted almost indefinitely by cold and inactivity; and it has been ascertained by Mr. Paget, that, "if the general development of the Tadpole be retarded by keeping it in a cold dark place, and if hereby the function of the blood-corpuscles be slowly and imperfectly discharged, they will maintain their embryonic

state for even several weeks longer than usual, the development of the second set of corpuscles will be proportionally postponed, and the individual life of the first will be, by the same time, prolonged."*

341. We see, then, that external agencies have a most important influence upon the length of the life, either of the entire organism, or of its constituent parts. The greater the intensity of vital activity which they excite, the less is its duration; for, so soon as the series of vital operations, which each cell or other integral element is adapted to perform, has come to a close, the very same agencies that excited and maintained them, hasten its decomposition and decay. Of this we have a characteristic example in the case of annual Plants, the length of whose term of life is inversely proportional to the amount of light, heat, &c., by which their vital activity has been called forth. And we see it also still more remarkably in the case of their seeds, which may retain their vital endowments for an unlimited period, provided the vegetative actions are prevented by the deficiency of warmth, moisture, and oxygen; but which, when called into germination, develope themselves into structures whose duration is extremely transient.—It does not seem an unfair inference, then, from these and similar facts, that the *Vital force* takes the place, in an Organised structure, of the *Chemical affinity*, which holds together the component particles of Inorganic bodies; and if this Vital force be nothing else than the *modus operandi*, in Organised bodies, of the very same forces which are termed Physical when acting through Inorganic matter, the relation between the two agencies seems to justify such a conclusion.† For, to take the case of the growing plant, so long as it is acted-upon by Heat and Light, and is supplied with nutritive materials, it continues to act upon these, and to extend its own organism by the appropriation of them, giving origin to new tissue, and thus developing an additional amount of Vital force; during the period of its most active growth, it shows little or no tendency to decay; but no sooner does the series of vital operations which it is fitted to perform, approach its termination, than the signs of degeneration show themselves, and the influence of Physical agencies is shown in promoting Chemical rather than Vital changes.

342. The operations in which the act of Nutrition appears essentially to consist, may be conveniently divided into two principal stages; the first of which, *Assimilation*, comprehends that gradual preparation for organisation, which the crude alimentary materials undergo whilst they are yet in a fluid state; the second, *Formation*, on the other hand, consists in the application of the assimilated or organisable particles to the generation of new tissues, or to the replacement of those which have become effete. This distinction cannot be recognised in the lower forms of either Vegetable or Animal existence, in which every component part executes both these operations alike, assimilating the nutritive matter, and either incorporating it with its own substance, or applying it to the production of new parts developed by its own vital endowments. It is in the higher Plants and Animals that we find distinct evidence, that the act of Assimilation may be performed by parts of the organism, which do not

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* "Lectures on Surgical Pathology," Vol. I., p. 13.

† See "Principles of General Physiology."

themselves apply the organisable material to the formation of tissue; and that the act of Formation may take place in parts, which have had no participation in the previous preparative changes. Such a modification is quite in accordance with the general rule of 'division of labour,' which has been so frequently alluded-to as a characteristic of the higher organisms.—Both these operations are purely *vital*. They have nothing in common with physical or chemical changes; and cannot be produced (so far as our present knowledge extends) except through the instrumentality of an organised structure.

343. It would seem as if, in the act of *Assimilation*, the plastic force is imparted by the solid tissues already formed, to the nutritive fluid in contact with them; for there can be no doubt that the fluid becomes possessed of properties which are themselves purely vital, and that its manifestation of these is most complete when it is in immediate relation with the living solids. Thus, the coagulation of the 'plasma' of the blood, and the formation of a fibrous tissue which is the result of that act when it is most perfectly performed (§ 374), can obviously be attributed only to the peculiar endowments of which the material has become possessed, subsequently to its introduction into the animal body; it takes place most perfectly, when the plastic material is poured-out upon the surface, or effused into the interstices, of living tissues; and it may be altogether prevented by such a violent 'shock,' as suddenly and completely destroys the vitality of the body. But we shall see reason to believe that there are certain organs, alike in the Animal and in the Vegetable, which are *specially* destined to effect the elaborating process; without superseding, however, the more general agency first alluded to.

344. In the act of *Formation*, a still higher measure of plastic force seems to be brought to bear on the same elements; since they are then enabled, not merely to assume a more perfectly-organised form, and to manifest endowments of a much higher character, but also to develope, in their turn, similar vital endowments in other nutritive materials. We may trace at least four distinct modes in which it takes place.—In the *first* place, the material may be applied solely to the *interstitial augmentation* of the existing elements of the structure; its component cells or fibres increasing in size without undergoing multiplication, and the whole organ being enlarged without the generation of any new integral part. This is probably the case with the leaves of Plants in general, which continue to enlarge, after the number of cells they contain appears to have ceased increasing; and it may also happen in some other instances; but in general, the enlargement of the cells, &c., already developed, takes place in conjunction with the *next* form of the nutritive process.—This, *secondly*, consists in the *multiplication* of the cells or other component parts, by the subdivision of those previously existing, or by outgrowth from them. Such appears to be the mode in which the most rapid increase of living structures takes place; and it is seen alike in the Plant and in the Animal, in the most complex as well as in the simplest forms of both. The type according to which this process has already been described as taking place in the lower Cellular Plants (§ 22), seems to be that on which it is performed even among the highest Animals: in the latter, however, it is especially during embryonic life (§ 73), and in

the development of entirely new parts at subsequent periods, that we meet with examples of it; still there are certain tissues, as Cartilage, in which it continues to take place throughout the whole of life.—In the *third* mode of formation, the new tissues seem to arise from certain 'germinal centres,' which appear to have the character of cell-nuclei; sometimes, perhaps, not having been themselves fully developed into cells, and sometimes being residual components of cells which have undergone transformation, but which leave to their nuclei the developmental power. Of this mode of formation, which seems peculiar to Animals, we have examples in the development of gland-cells from the nucleus at the cæcal extremity of the follicle or tubule from which they are to be cast-forth (§ 407), and in the production of the component cells of muscular fibrillæ from the nuclei contained within their enclosing tube. Whether the epidermic and epithelial tissues generally take their origin in germinal centres contained in the 'basement membrane,' as maintained by Prof. Goodsir, or are developed in the fourth mode, has not been yet certainly determined. In the adult condition of animals, in which no new parts are formed, but maintenance of those already existing is alone required, this mode of formation is undoubtedly more common than any other. For such 'germinal centres' or 'cytoblasts' are scattered through a large part of the fabric, their relative abundance in different organs being nearly proportional to their respective activity of growth, and their disappearance being (as Mr. Paget has justly remarked) a sure accompaniment and sign of degeneration.—But, *fourthly*, new tissue may be formed at once by the coagulation of the plastic fluid, without the direct intermediation of pre-existing cells or germinal centres (§ 387); but it usually possesses a very low degree of vitality; for, if it be developed into cells, these usually show a peculiar proneness to degeneration; whilst, if it possess the fibrous type, it consists of little else than an aggregation of similar particles into homogeneous fibres (§ 388). This mode of formation is rare in Plants, and is most commonly seen in Animals in the reparation of injuries.

345. Under whichever of these methods the Formation of tissues may be performed, the same general conditions are required.—In the *first* place, it is requisite that a due supply of the material be afforded, in a state in which it can be appropriated. The degree in which the formation of each tissue is dependent upon the previous preparation of its nutritive materials, seems to vary greatly. Thus among the lower tribes of Plants, in which there is little or no 'division of labour,' every cell can effect the preparative operations, as well as appropriate the material so prepared; whilst in the higher, a large part of the organism is dependent for its pabulum upon the materials supplied elsewhere. But we shall presently see (§ 359), that out of the very same organic compounds, the different cells of the higher Plants can elaborate a great variety of few products, differing widely in their chemical character; so that they must retain a certain degree of converting power. Other circumstances being the same, the activity of growth is proportional to the abundance of the nutritive material, provided that the formative power be not wanting. This is especially seen in Plants, in which there are fewer counteracting agencies; and it is, in fact, the foundation of a large part of the art of Cultivation, which aims especially to accelerate the growth of the

entire plant, or to augment the growth of some particular part, by increasing the supply of the aliment which it may require. But we have also very characteristic examples of it in Animals; such as the increase in the Adipose tissue, when the food has been abundant in quantity and rich in quality; the increase in the size of Glands, when the blood contains an unusual quantity of the special product to be eliminated by their agency; and (according to many eminent Pathologists), the development of abnormal growths (such as Cancer, Tubercle, Lepra, &c., &c.), which remove particular morbid matters from the current of the circulation, with a rapidity proportional to the supply of the peculiar pabulum which their cells respectively require. It seems probable, indeed, that the Animal tissues have less *converting* power than those of Plants; and that not only each tissue, but each part of the same tissue, *selects* some different material from the blood. For there are certain morbid matters, whose presence in the blood is manifested by the perversion of the nutritive process in certain spots only of the body, these spots being similar in size and situation on the two sides; so that it would seem that the only parts of any tissue which are really identical in composition, are those which occupy symmetrical positions on the opposite halves of the body.* Now in the healthy state, as in those diseased conditions which afford more striking exemplifications of this principle, every part of the body, by taking from the blood the peculiar substances which it needs for its own nutrition, thereby removes from it a certain part of its constituents, which would interfere with the nutrition of the rest of the organism, if retained in the circulation. And this, as Mr. Paget has well remarked, seems to be the purpose answered by the development of many structures that perform no ostensibly-useful part in the economy; such as rudimental organs of various kinds, the *lanugo* or downy covering of the human fœtus which falls off some time before birth, and the coat of hair which is formed in many of the lower Mammals during fœtal life, and which gives place before birth to a more complete coat of a different colour. The development of these and other structures, for which no other purpose can be assigned, may be fairly regarded, on the principle which has been now laid-down and illustrated, as resulting from the presence of their peculiar materials in the blood, and as leaving it fitter, by the removal of them, for the nutrition of other parts, or as adjusting the balance which might else be disturbed by the formation of some other part. "Thus," to use Mr. Paget's own words,† "they minister to the self-interest of the individual, while, as if for the sake of wonder, beauty, and perfect order, they are conformed to the great law of the unity of organic types, and concur with the universal plan observed in the construction of organised beings." When the due supply of nutritive material is *not* afforded, imperfect or deficient formation must be the result; and this is probably the explanation of the atrophy which normally occurs in the course of the life of higher animals, in many organs, which at earlier periods of life were of considerable size and importance, such as the thymus gland, the ductus arteriosus and venosus, the mammary glands, &c.

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* See Dr. W. Budd's admirable paper on 'Symmetrical Diseases,' in the "Medico-Chirurgical Transactions," Vol. XXV.; and Mr. Paget's "Lectures on Surgical Pathology," Chap. I.

† Op. Cit., Vol. I., p. 26.

346. In the *second* place, the formative process is mainly dependent upon a due supply of Heat. This agent has been commonly regarded as the mere *stimulus* to its activity; but there seems adequate reason for the belief, that Heat, acting through a substance previously organised, *itself becomes* the formative power (GENERAL PHYSIOLOGY).* This much, however, is certain; that the activity of *growth* bears a very close relation to the temperature of the fabric, so that the formative processes may be artificially retarded by cold or accelerated by warmth; and it further appears that *development* requires a higher temperature (as it certainly seems to depend on a higher measure of vital force) than simple *growth*. Thus it is found that the completion of the metamorphosis of certain Insects, is aided by the generation of heat in 'nurses,' whose bodies impart it to those which they tend (§ 447); and the reproduction of lost parts in the Triton (§ 474) requires a temperature higher by many degrees than that which suffices to maintain a considerable degree of general nutritive activity. Hence we see that the very same agent which exerts so remarkable an influence on the duration of the life of the tissues, exerts a corresponding influence on those processes by which their disintegration is compensated; and the perfect balance between waste and repair is thus maintained. In Plants, indeed, we see this beautiful adjustment extending still further back; for the Heat which promotes the formative processes is accompanied (when not artificially supplied) by a corresponding amount of Light; and these two agents, in proportion to the intensity of their operation, accelerate the absorption of fluid by the roots (§ 328), and also produce a corresponding increase in the supply of carbon fixed by the leaves.

2. *Nutrition in Vegetables.*

347. The elementary phenomena of Vegetable Nutrition are in many respects best studied in those simple Cellular Plants, of which every cell performs all its essential operations, and is entirely independent of its fellows; to these, therefore, we shall first direct our attention.—So far as we at present know, every cell, like every individual Plant or Animal, is the product of a previous organism of the same kind; there being no valid reason to believe that any organised fabric, even of the simplest kind, can originate in the combination of inorganic elements, without the intermediation of a substance already endowed with vitality. This substance, however, may not be a definite 'germ-particle;' for it seems often to be nothing else than a fragmentary portion of the liquid contents of some pre-existing cell. The first stage in the development of any such body into a new cell, must consist in the production of the requisite *pabulum* or material, out of those simple binary compounds which serve as food to Plants (§ 120); and it may be conceived without any great improbability, that in this operation the germ-particle or its representative acts a part analogous to that of a 'ferment,' save that the metamorphosis which it promotes is a step in the ascending series (*i. e.*, from inorganic matter up to organic compounds), instead of being in the downward direction (*i. e.*, from organic compounds towards inorganic bodies), as is the case with that of ferments in general. It is only under

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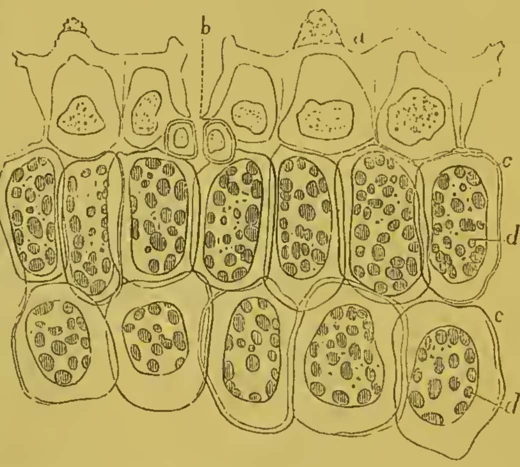
* See also the Author's Memoir 'On the Mutual Relations of the Vital and Physical Forces,' in the "Philos. Transact.," 1850.

the influence of light, however, that this change can take place; and the amount of the new compounds thus generated, as measured by the quantity of oxygen given-off in the act of their production, is strictly conformable, *cæteris paribus,* to the degree in which the decomposition of carbonic acid is promoted by that agent. This result of the incipient nutritive operations of the simple Cellular plants, is made obvious by the frothing-up of the green scum which floats upon ponds, ditches, &c., when the sun's rays fall upon the surface; the bubbles of gas thus disengaged being found upon analysis to consist of oxygen. It will be presently enquired, what are probably to be regarded as the first compounds thus generated (§§ 359—362); little doubt can exist, however, that they are either the vegetable acids, or the neutral components of their tissues.* For in every situation in which Vegetable nutrition is taking place, *dextrine* (or starch-gum) and an *albuminous compound* are present, the latter being especially abundant in young and rapidly-growing parts; whilst it is only in the more advanced stage of life of cells which have ceased to perform any more active functions, that we meet with other products, whose composition is less immediately related to that of the cell-walls themselves. Of the two products just named, the latter is the one that chiefly ministers to the formation of the 'primordial utricle' (Fig. 159, *dd*), which is the immediate investment of the contents of the cell, and which is undoubtedly the part of its wall that is most actively concerned in its vital operations; whilst the former, which is always present in much greater abundance, is the pabulum at the expense of which the outer or cellulose layer (*cc*), is generated around this, its thickness being augmented from time to time by additional exudations.

Fig. 159.



Section of leaf of *Agave,* treated with dilute nitric acid, showing the primordial utricle contracted in the interior of the cells;—*a*, epidermic cells; *b*, boundary cells of the stoma; *c*, cells of parenchyma; *d*, their primordial utricles.

348. Previously to their appropriation, however, by the solids of the cell, these materials are united (together, it appears, with sugar and oleaginous particles) into a peculiar viscid granular fluid, which has received the designation of *protoplasma,* and which appears to be in immediate vital relation with the growing organism. This fluid is

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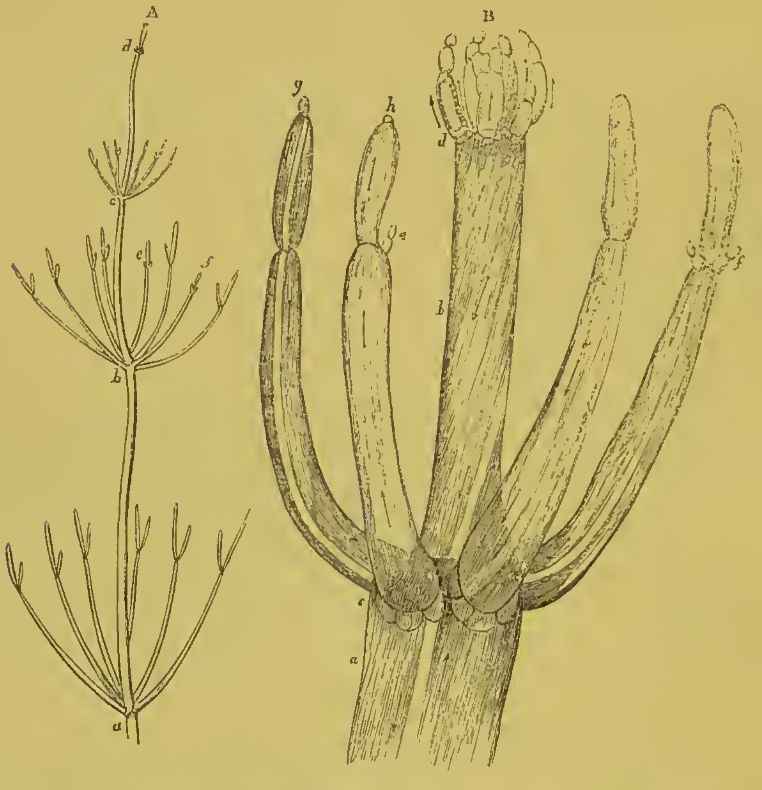
* The production of green-colouring matter has been very commonly supposed to constitute one of the early stages in the 'ascending' or 'progressive' metamorphosis; and it is not surprising that such should be the current opinion, when it is remembered that this occurs in the parts most exposed to light, and that its amount seems to be a measure of the influence of that agent. But the chemical composition of 'chlorophyll,' so far as it has been ascertained, bears a much closer resemblance to that of oil and wax, than to that of the less deoxidised compounds; and it is probable, therefore, that its production accompanies, or is subsequent to, that of the tissue-forming substances, instead of being antecedent to them. See Mulder's "Chemistry of Animal and Vegetable Physiology," p. 281.

coloured yellow by iodine, and coagulated by alcohol and acids; in very young cells, it occupies nearly the entire cavity, certain *vacuoles* only being perceptible, which are occupied by a more watery fluid or 'cell-sap;' but with the advance of the life of the cell, these *vacuoles* increase in size, and coalesce, so that at last the watery cell-sap almost entirely takes the place of the protoplasma, which merely forms a lining to the primordial utricle. A very remarkable movement is often seen to take place in the protoplasma, which is known under the name of 'rotation.' This was first observed in the long tubular cells of the *Characeæ*, a little group belonging to the class of Algæ; and they still afford the best illustration of the phenomenon.—Each cell, in the healthy state, is lined by a layer of green oval granules, which cover every part of its wall save two longitudinal lines that remain nearly colourless (Fig. 160, B); and a constant stream of semifluid matter, containing numerous jelly-like globules, is continually flowing over this green layer, the current passing up one side, changing its direction at the extremity, and flowing down the other side, the ascending and descending spaces being bounded by the transparent lines just mentioned. That the currents are in some way directed by the layer of granules, appears from the fact noticed by Mr. Varley,* that if accident should damage or remove them, near the boundary

Fig. 160.



Nitella flexilis:—A, stem and branches of the natural size; *a, b, c, d,* four verticils of branches issuing from the stem; *e, f,* subdivision of the branches;—B, portion of the stem and branches enlarged; *a, b,* joints of stem; *c, d,* verticils; *e, f,* new cells sprouting from the sides of the branches; *g, h,* new cells sprouting at the extremities of the branches.

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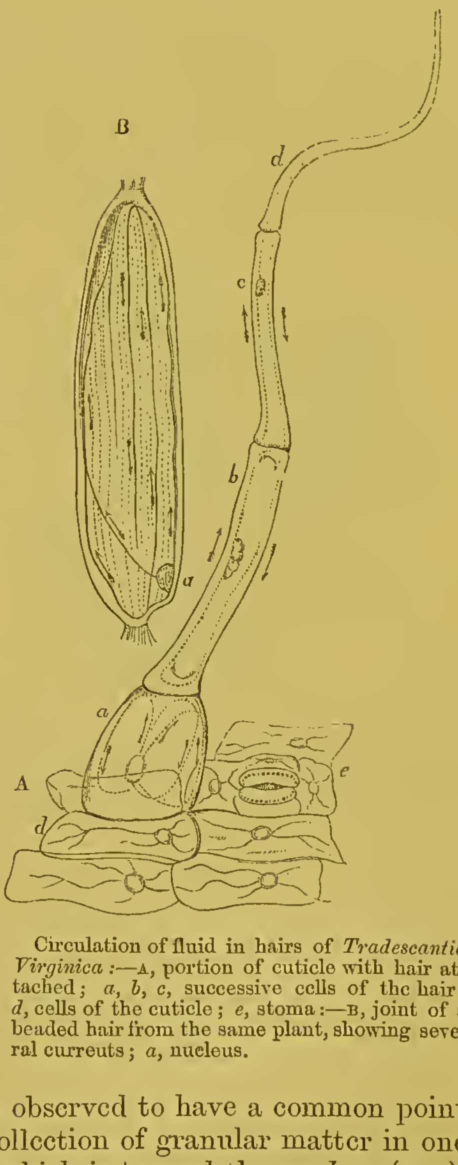
* "Transactions of the Microscopical Society," 1st Series, Vol. II., p. 99.

between the ascending and descending currents, a portion of the fluids of the two currents will intermingle by passing the boundary; whilst, if the injury be repaired by the development of new granules on the part from which they had been detached, the circulation resumes its regularity, no part of either current passing the boundary. In the young cells, however, the rotation may be seen, before their granular lining is formed. The rate of this circulation is affected by anything which influences the vital activity of the plant; thus, the movement is accelerated by moderate warmth, whilst it is retarded by cold, and may be at once checked by a slight electric discharge through the plant. The moving globules, which seem to consist of starchy matter, are of various sizes; being sometimes very small, and of definite figure, whilst in other instances they are seen as large irregular masses, which appear to be formed by the aggregation of smaller particles. If the cell be carefully tied across, the current is re-established within a short time in each segment, as if the cell had naturally subdivided itself.—This phenomenon may also be well studied in certain aquatic Phanerogamia, belonging to the families *Nayadaceæ* and *Hydrocharidaceæ;* the *Vallisneria spiralis*, which belongs to the last-named of these, exhibiting it in a peculiarly striking manner. The rotation is by no means confined, however, to aquatic plants, for it may be readily detected in the hairs of Flowering-plants, many of which afford very beautiful examples of it, and it has been observed also in the young cells of leaves, fruits, and other parts; so that it may with probability be regarded as existing in every vegetable cell at a certain stage of its development. The current is seldom so broad, however, as in the instances already described; and usually presents itself as a thread-like stream, passing through a stratum of motionless matter. This stream may be single, passing up one side of the cell, and down the other, as is usually the case in long and tubiform cells (Fig. 161, A, *b*, *c*;) but several distinct currents may exist in the same cell, and these are observed to have a common point of departure and return,—namely, a collection of granular matter in one mass, attached to the wall of the cell, which is termed the *nucleus* (B, *a*). Here, too, it would appear, that the currents are connected with the general

FIG. 161.

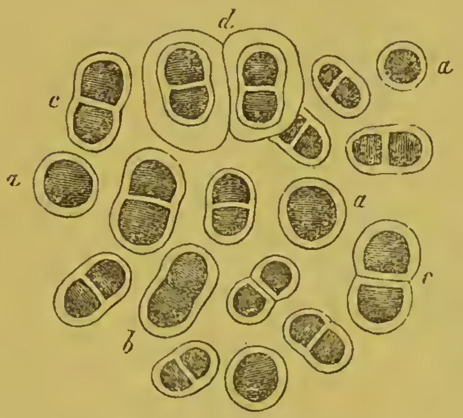


Circulation of fluid in hairs of *Tradescantia Virginica*:—A, portion of cuticle with hair attached; *a*, *b*, *c*, successive cells of the hair; *d*, cells of the cuticle; *e*, stoma:—B, joint of a beaded hair from the same plant, showing several currents; *a*, nucleus.

activity of the life of the cell, and that their cessation indicates the cessation of its formative powers; and from the manner in which they are connected with the 'nucleus,' it would seem that this, where it exists, is to be regarded as the centre of the vital activity of the cell. Although such a nucleus is to be found, however, in a very large proportion of Vegetable cells, yet its absence in some instances is a matter of equal certainty with its presence in others; and as these do not manifest any inferiority of vital power, the nucleus is obviously not essential. Perhaps we should be correct in regarding it as concentrating in itself a portion of the forces which are elsewhere diffused through the entire 'protoplasma' and 'primordial utricle,' rather than as having any peculiar powers; and this idea is confirmed by the facts presently to be stated, in regard to the production and multiplication of cells.

349. The formative activity of the Plant-cell may be manifested in various ways. The cell may develope itself more fully as an individual; appropriating its protoplasma to the extension of its walls, so as to augment its size; or solidifying its thin coats by deposits arranged concentrically or otherwise upon their interior, so as gradually to occupy a considerable part of its cavity; or filling this cavity with products of various kinds, which it elaborates for itself from its primitive pabulum. Or, on the other hand, it may give origin, by its own subdivision, to two or more cells, which in their turn may undergo a like multiplication; the life of the primary cell being thus (so to speak) carried on, and distributed through a vast aggregation of organisms resembling itself.* The most common method of multiplication is the subdivision of the original cell into two halves, such as is seen very characteristically in the *Hæmatococcus binalis* and others of the humblest forms of vegetation, in which every cell, being capable of existing by itself, is commonly regarded as a distinct individual. The cells of this little plant are originally of a globular form (Fig. 162, *a*); and the first step in the process of subdivision is their elongation into an oval shape, and the appearance of a slight constriction round them, as seen at *b*. This constriction indicates the tendency of the 'endochrome' (or mass of coloured cell-contents) to separate

Fig. 162.



Various stages of development of *Hæmatococcus binalis*:—*a*, *a*, simple rounded cells; *b*, elongated cells, the endochrome preparing to divide; *c*, *c*, cells in which the division has taken place; *d*, cluster of four cells formed by a repetition of the same process.

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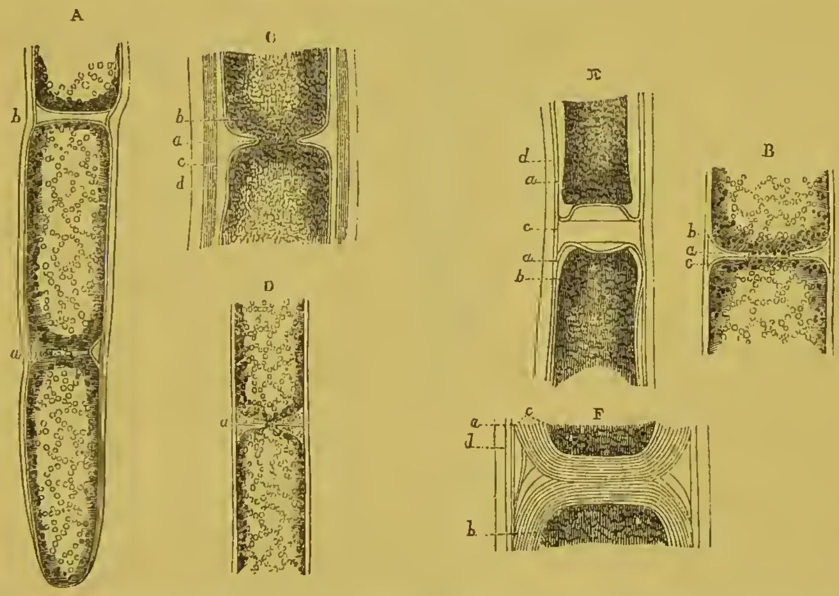
* It is customary to speak of the original cell as the *parent* or *mother*, and of the cells formed by the subdivision of its contents as the *offspring* or *daughters*. This phraseology, however, is peculiarly liable to convey a wrong impression; since the terms 'parent' and 'offspring,' in their proper acceptation, convey an idea that is essentially different; and the word 'mother-cell' should not be used where there is no sexuality (see Chap. XI., Sect. 1.) In the one case, the vital endowments of the primary cell are transmitted by direct continuity to the entire aggregation (however numerous) into which it may develope itself; whereas the resultant of the true generative process, for which the concurrent action of two cells is always required, is (so to speak) a new creation.

into two halves, each included, it would appear, in an envelope of its own, so that two secondary cells are now included within the external wall of the primary; and after this has been effected, the contiguous portions of the two 'primordial utricles' appear to develope or secrete a thick partition between them, so that the two secondary cells are now completely divided, as seen at *c, c*. An increase of a somewhat similar but less condensed secretion on their exterior, forms a mass of mucus, in which the cells are imbedded; and these are frequently carried, by the interposition of this new substance, to a considerable distance from each other, as is shown at *d*, where each of the first pair of secondary cells has itself undergone a similar subdivision.—This process may also be well studied in the *Confervæ*, which are filamentous aquatic plants, each filament composed of a single file of cells, adherent to each other end-to-end; and we shall derive from the examination of one of these a further insight into some stages of the process. The first step is here seen to be the subdivision of the 'endochrome,' and the inflexion of the 'primordial utricle' around it (Fig. 163, A, *a*); and thus there is gradually formed a

Fig. 163.



Process of cell-multiplication in *Conferva glomerata*:—A, portion of filament with incomplete partition at *a* and complete partition at *b*;—B, commencement of the formation of a partition; C, more advanced stage; D, the separation nearly complete; E, the two primordial utricles completely detached, and cell-membrane deposited between them; F, successive layers of cell-membrane, making up the thickness of the partition. In the last five figures, *a* indicates the primordial utricle; *b*, the endochrome; *c*, the cell-membrane, and *d*, the mucous investment.

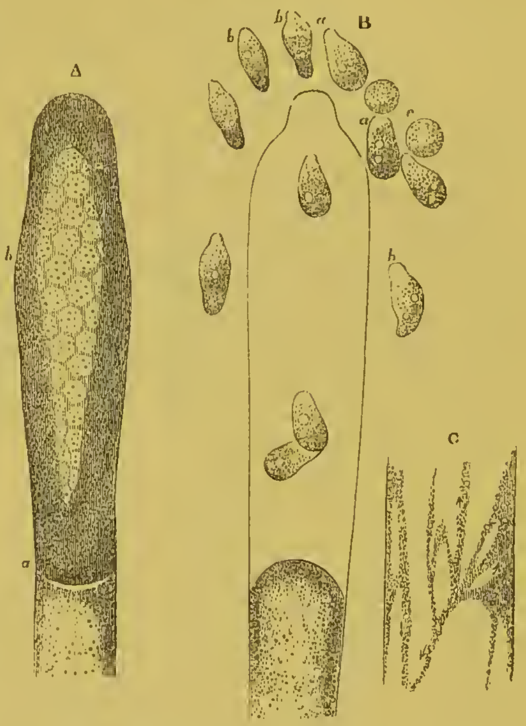
sort of hour-glass contraction across the cavity of the primary cell, by which it is divided into two equal halves (B). The two surfaces of the infolded utricle produce a double layer of permanent cell-membrane between them; and the formation of this may be seen to commence, even before the complete separation of the cavities of the twin-cells (D). This deposition is not confined, however, to the contiguous surfaces of the secondary cells, but takes place over the whole exterior of the primordial utricle; so that the new septum is continuous with new layers that are formed throughout the interior of the original primary cell (C).

350. The foregoing is the method according to which the extension of Vegetable structures from cells already in existence, most commonly takes place. Among the lower Algæ, for example, we find the single cell giving rise to an amorphous cluster (Fig. 10), to a prolonged filament (Fig. 11), or to flattened leaf-like expansion (Fig. 12), according to the mode in which the subdivision occurs, and to the degree in which the new cells remain attached to each other.—It does not appear that in this process the 'nucleus' performs any essential part; for we find it taking place where no nucleus can be distinguished, in virtue, it may be surmised, of a sort of mutual repulsion between the two halves of the endochrome, which leads to their spontaneous separation. Where a nucleus is present, this also undergoes subdivision at the same time with the endochrome, so that half of it is appropriated by each of the secondary cells.—But we sometimes observe that secondary cells originate in little bud-like prominences on the surface of the primary, developed in continuity with that from which they arise. This is well seen in the *Conferva glomerata,* a common species, which increases not merely (like other Confervæ) by the repeated subdivision of the cells at the extremity of its filaments, but by the origination of new cells from every part of their surface. A certain portion of the primordial utricle seems to undergo increased nutrition; for it is seen to project, carrying the outer cell-wall before it, so as to form a protuberance, which sometimes attains considerable length before any separation of its cavity from that of the primary cell begins to take place. This separation is gradually effected, however, by the infolding of the primordial utricle, just as in the preceding case; and thus the endochrome of the secondary cell is completely severed from that of the primary, and its independent existence may be said to begin from that time. We may consider this process of 'budding' as differing from that of 'subdivision' only in this,—that whilst in the latter case the individuality of the primary cell is lost by the *equal* subdivision of its cavity into two similar parts, it is retained in the former through the *unequal* division of the cell, of which only a small portion is pinched-off (so to speak) to form the secondary cell, whilst the greater part remains unaltered. Of the extent to which the multiplication of cells by this budding process takes place among plants, we have as yet no certain knowledge. It is obviously the regular method of growth among the *Characeæ,* in which the long tubiform cells that form the axis give-off, at their points of junction with each other, circular rows of buds, from each of which is developed a whorl of lateral branches. And the same mode of increase is observable among the 'ferment-cells' of the Yeast-plant, which, whilst rapidly multiplying under favourable circumcumstances, shoot-forth little buds from one or even both extremities, from each of which a secondary cell is developed. There is no reason to believe that in this process the 'nucleus' takes any direct share; since the evolution of buds may take place from cells destitute of nuclei; and even where nuclei exist in budding cells, they do not seem to be specially connected with the process, since the buds are not observed to originate in or near them.

351. In cases where a very rapid production of new and independent cells is requisite, it would seem to be effected by the separation of the contents of the primary cell into numerous parts, each of which acquires for

itself a covering of cell-membrane; so that a whole brood of secondary cells may thus be at once generated in the cavity of the primary cell, which subsequently bursts and sets them free. Of this plan we have the most characteristic examples in the formation of the 'zoospores' of the Protophyta (§ 22). Thus in *Achlya prolifera*, a plant composed of tubiform cells, which grows parasitically upon fish, the end of the filament dilates into a large cell, the cavity of which is cut-off from the rest by the formation of a partition; and within this dilated cell, an irregular circulation of granular particles can for a time be distinguished (Fig. 164, c). Very speedily, however, it appears that the 'endochrome' is being broken-up into a large number of distinct masses, which are at first in close contact with each other and with the walls of the cell (A), but which gradually become more isolated, each seeming to acquire a proper cell-wall; they then begin to move about within the primary cell; and, when quite mature, they are set free by the rupture of its wall (B), to go forth and form new attachments, and to acquire for themselves the materials of development into tubiform cells resembling those from which they sprang. A similar process may be observed in the production of the 'zoospores' of Confervæ and Algæ in general; usually taking place, however, upon a smaller scale, and the number of new cells being generally less, than in the instance just quoted. And there appear to be some cases among the higher plants, in which primary cells give origin to a new brood in their interior, by a process somewhat similar, without the successive duplication which is certainly the more usual method of the production of 'cells within cells,' or 'endogenous multiplication.' This seems the case, for example, in the 'embryo-sac' of Flowering-Plants (§ 504); which at one time contains only a mixture of albuminous and starchy matter, but which is afterwards filled-up by a mass of cells, that have incorporated these materials into their own substance, forming the 'endosperm.' According to Nägeli, who has recently investigated this process with much care, the following are the essential points in its history. Minute globular particles of perfectly homogeneous matter, varying in diameter from 1 to 4-1000ths of a line, seem to be first formed in the midst

Fig. 164.



Development of *Achlya prolifera*:—A, dilated extremity of a filament *b*, separated from the rest by a partition *a*, and containing young cells in progress of formation; B, conceptacle discharging itself, and setting free young cells, *a*, *b*, *c*; —C, portion of filament showing the course of the circulation of granular contents.

of the mucilaginous contents of the embryo-sac; larger globular bodies are apparently produced by the aggregation of other (nitrogenous?) particles around these, forming the nuclei of the future cells. Each of these nuclei seems to attract around it a greater or smaller quantity of the contents of the primary cell; and over this a membrane is subsequently generated.* Thus the history of such a formation is very nearly the same with that which we have traced in the inferior Cryptogamia; and it may be that even in the latter, the formation of nuclei, round which the contents of the primary cell group themselves, may be really the first stage in the production of the mass of secondary cells.

352. The first *visible* stages of the development of new cells, however, do not always take place in the interior of a pre-existing generation; for cells sometimes appear to originate *de novo*, in that mixture of starchy and albuminous fluids, which, being the appropriate pabulum for Vegetable cells, has been denominated *protoplasma*. This protoplasma, however, must have always been elaborated by cell-agency; so that, even if the young cells appear to be developed quite independently in its substance, they must really be regarded as the offspring of the cells which formed it. In some instances which have been regarded in this light, it is probable that the protoplasma was contained in a cellular parenchyma which escaped observation through its extreme delicacy: whilst in other cases, there can be no doubt that definite cell-germs had been prepared and set free with the protoplasma, escaping observation on account of their minuteness.

353. There is evidence that the process of Cell-production may take place with a rapidity almost inconceivable. Extensive tracts of snow, in alpine and arctic regions, have been seen to be suddenly reddened by the cells of the little *Protococcus nivalis;* and there are some minute blood-red Fungi, which occasionally make their appearance in almost equal multitudes upon the surface of every organic substance. Almost every one is familiar with the appearance of certain more elevated forms of fungous vegetation, which shoot-up in the course of a single night, and seem to melt-away before the morning sun. A specimen of *Bovista giganteum*, a large fungus of the *puff-ball* tribe, has been known to grow in a single night from the size of a mere point to that of a huge gourd; and from a calculation of the average size of its cells, and of the probable number contained in the full-grown plant, it has been estimated that they must have been generated at the rate of *four thousand millions* per hour, or more than *sixty-six millions* per minute. In all such cases, the amount of solid matter present in the tissues bears a very small proportion to the fluids.—A very rapid growth of leaves may be occasionally noticed; thus the leaf of *Urania speciosa* has been seen to lengthen at the rate of from 1½ to 3½ lines per hour, and even as much as from four to five inches per day. It is doubtful, however, how much of this result may be attributed to the formation of new cells,

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* See Nägeli 'On the Formation of Vegetable Cells,' in the "Reports and Papers on Botany," published by the Ray Society, 1845 and 1849; also Mohl's "Principles of the Anatomy and Physiology of the Vegetable Cell," translated by Mr. Henfrey; and Braun on 'Rejuvenescence,' published by the Ray Society in "Botanical and Physiological Memoirs," 1853.

and how much is due to the enlargement of those of which the leaf was previously composed.

354. Such cells as those now described, present themselves not only as the constituents of those simplest Vegetable organisms, in which every cell can maintain an independent existence; but also as the chief, and frequently the sole, components of fabrics of much higher rank, and of much greater complexity of structure. Thus we do not meet with any other forms of tissue than those referable to the simple Cellular type, in any of the Algæ, Lichens, Fungi, or Mosses: whilst in Ferns and Flowering Plants, we find this tissue not merely in the soft substance of the leaves, flowers, and fruits, but also in the stem, branches, and roots; uniformly making-up the chief part of the organs most actively concerned in the vital operations, and being almost the sole component of young and growing structures. The other tissues—namely, Woody Fibre, and the various kinds of Vessels and Ducts,—may all be considered as metamorphosed cells; the progressive stages in the transformation being made-out with little difficulty. But in undergoing this change, they seem to lose some of the distinguishing attributes of the primary type; for it is in the *cellular* portions of the Plant alone, that the multiplication takes place, whereby new parts are produced. In all the more highly-organized forms of Vegetable structure, however, the development of the cells that are to form the more permanent parts of the fabric, and the multiplication of those which are evolving themselves into new organs, take place at the expense of a plastic fluid which is elaborated in temporary organs expressly set apart for the purpose; and the history of this elaboration has now to be traced.

355. In the greater number of *Vascular* Plants, there is no doubt that the greatest proportion of the fluid imbibed into the system is derived from the soil surrounding the roots; and that it holds in solution carbonic acid and ammonia, from the combination of whose elements are produced the proximate principles, gum, sugar, albumen, &c., at the expense of which the tissues are generated. It would seem that the fluid thus absorbed is in all plants nearly the same, under corresponding circumstances, except as regards the mineral ingredients of the soil (§ 120); and that, provided this contain an adequate supply of the above-named compounds, the presence of organic matter in it is not peculiarly favourable to growth. Even in the roots, however, the fluid that is passing upwards through the axis is found to contain dextrine, sugar, and vegetable acids;* and during its upward ascent, its specific gravity still further increases, and the quantity of its solid components becomes sensibly greater. If the results of experiments and observations, however, on the functions of the leaves (§§ 268—271), be duly considered, it seems difficult to avoid the conclusion, that the greatest addition to the materials for the formation of the solid tissues of plants is made through *their* agency (or by that of other leaf-like surfaces); and that the greater part of the process of conversion of the oxygen, hydrogen, carbon, and nitrogen, obtained by the

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* It is inferred by Prof. Schleiden and his followers that these are generated by the tissues among which the liquid is diffused, which begin to exert an assimilating power upon the crude sap, as soon as it is brought within their reach. There are cogent objections, however, to such an hypothesis; and the fact may be as well explained in another way (§ 202).

plant from the water, carbonic acid, and ammonia, which it imbibes, into organic compounds, is effected by their instrumentality. We have seen that of the water taken-in by the roots, a large proportion must necessarily be exhaled by the leaves; since, in order to obtain the requisite supply of the matters which are sparingly dissolved in this liquid, the plant must absorb far more of it than it can apply to its own use. Hence the crude sap brought to the leaves undergoes a double change; a large proportion of its water being got rid of, whilst a great addition is made to its carbon; and thus a great increase is presented in the proportion of organic compounds which the 'proper juices' of the leaves contain. These proper juices appear to furnish the chief part of the *pabulum*, at the expense of which the development of new parts takes place in every part of the organism; for although it may not be distributed, as some have supposed, by any regular 'descending current' (§ 202), yet it is impossible to account for the large quantity of additional carbon taken-in by the leaves, unless it be thus applied, since it is certain that these organs themselves do not undergo any proportional increase, during the period when they are most actively performing the function of aeration.

356. That a marked difference exists between the crude ascending sap whose materials are supplied by the roots, and the 'proper juices' whose formation thus seems chiefly to depend upon the leaves, is shown in a variety of ways. Thus, the inhabitants of the Canary islands tap the trunk of the *Euphorbia canariensis* and obtain a refreshing beverage from the ascending current, although the proper juice of the plant is of a very acrid character. The phenomena of *vegetable parasitism* have a peculiar interest when viewed with reference to this subject. The Phanerogamic parasites may be arranged under two groups; those provided with leaves, belonging for the most part to the order *Loranthaceæ* (or mistletoe tribe); and those which are destitute of leaves, such as the *Cuscuta* (dodder), *Orobanche* (broom-rape), and *Lathræa squamaria.* Now the plants of the first group may be regarded as natural grafts, organically uniting themselves with their stock; for the wood and bark of the Mistletoe grow in continuity with the wood and bark of the tree to which it has attached itself, although the line of demarcation between the two may be seen when a vertical section is carried down through the part where they meet. It is obvious that it must receive its supply, like the branches of the stock itself, from the current of sap ascending in the latter; and that this must be converted, by the elaborating action of its leaves, into the materials of its growth. On the other hand, the leafless parasites attach themselves to the *bark* alone, by means of suckers which apply themselves to its surface, or of fibres which penetrate into its substance; and it seems obvious that, as they are not able to elaborate sap for themselves, they are dependent for their support, not upon the crude ascending current, but upon the 'proper juices' of the plants on which they live. And this view derives confirmation from the fact, that whilst the *leafy* parasites will grow almost indifferently upon a great variety of trees, their ascending sap differing but little in quality, the *leafless* parasites are much more limited in their range; each kind being usually restricted to a few species whose 'proper juices' are suitable for its support, and those of other plants not being adapted to its nutriment.

357. The leaves of the higher Plants may be regarded, then, as the chief *assimilating* organs, by which the materials are prepared for the *formative* processes that take place in different parts of the fabric; the essential pabulum of the vegetable tissues being the *protoplasma* (§ 348), containing saccharine, gummy, and albuminous matters in a peculiar state of combination, which is found in all rapidly-growing parts, and from which it is probable that each component cell of these tissues can elaborate for itself the peculiar compounds which it is destined to contain. And thus it happens that the growth of a 'stock' is not changed from its natural method, by the somewhat different quality of the proper juice that may be supplied by the leaves of a 'graft'; nor does the mistletoe impart any of its peculiarities to the branch of the tree with which it has united itself. From the very same pabulum, the wood of the mistletoe and that (*e. g.*) of the apple grow after their respective fashions; just as in the different parts of the mistletoe itself, the wood grows after one pattern, the bark after a second, the leaves after a third, the flowers after a fourth, and the fruit after a fifth. Every growing part, in fact, turns to its own account the 'pabulum' which it receives, and forms it into its own peculiar tissues. This 'pabulum' appears to be especially diffused through all the *cellular* portion of the fabric; and it is in this, as formerly explained, that all new formation originates. Thus we find new leaf-buds in the *Exogenous* stems of Dicotyledons (§ 29) developing themselves as extensions of the medullary rays; whilst in the (so-called) *Endogenous* stems of Monocotyledons, they spring from the general cellular mass of the axis; and in the cells of the parts from which they spring, we usually find a much larger accumulation of starchy and other nutritious materials, than could be derived from the quantity of ascending sap attracted towards them, before exhalation is actively established by the expansion of the buds.

358. The addition to the central axis, again, is effected in Dicotyledons by the continual growth and transformation of the *cambium-layer*, which intervenes between the last-formed layers of wood and bark. The cambium was formerly supposed to be a mere glutinous sap, and various notions were entertained in regard to the mode of its conversion into the new wood; but it is now quite ascertained that the cambium is really a mass of young cells turgid with protoplasma, and that as the inner layers of these are converted into fibro-vascular bundles, they continue to increase by the multiplication of cells on the outer side; and thus there is an absolute continuity of growth between the inner and outer parts of the axis, although, from the vegetative functions being periodically suspended in trees which cast-off all their leaves at once, lines of demarcation are more or less distinctly left between the portions formed at successive epochs. Thus are produced the so-called 'annual layers' in these stems; which are not, however, to be regarded as by any means *uniformly* indicating the number of years during which a stem or branch has been growing. For there are many trees in tropical climates, whose leaves are thrown-off and renewed twice or even thrice in every year, or five times in two years; and as the whole series of nutritive operations then receives a check, it cannot be doubted that a new line of demarcation will be left by every exuviation. Even in temperate climates, the same thing may be occasionally observed; thus the author has known a long

continuance of heat and dryness in the early part of the summer, to be followed by the entire exuviation of the leaves of trees growing in exposed situations; a new covering of leaves making its appearance within a few weeks afterwards. And temporary checks to the vegetative processes may arise from other sources; thus the growth of the larch, which naturally thrives in cold and moist situations, is stopped by heat and dryness; and the author has been assured by a competent authority, that he has ascertained by actual observation that two thin layers of wood have been formed by larches, instead of a single thick one, when the nature of the season had been such as to occasion a prolonged interruption. On the other hand, in 'evergreen' trees, in which the leaves are not all cast-off at once, the lines of demarcation are usually much less distinct, since the growth of the cambium-layer is not at any time completely stopped, except by intense cold. As the additional wood is always developed on the exterior of that previously formed, it is obvious that the term *Exogenous* may be appropriately applied to this mode of growth; it has been also designated as growth by *indefinite* fibro-vascular bundles.—On the other hand, in the stems of Monocotyledons, the fibro-vascular bundles once formed are not susceptible of increase, and they are therefore said to be *closed.* Hence the new bundles are not developed in continuity with the old, but take their origin in the midst of that part of the cellular mass of the stem which is in closest connection with the new leaves; and instead of extending through the entire axis, so as to augment its diameter from the extremities of the branches to those of the roots, they pass towards its exterior at no great distance from the summit, and there terminate, so that the lower part of the stem undergoes no augmentation. To these stems, therefore, the term *Endogenous* cannot be justly applied; and it should be dropped altogether.

359. But besides ministering to the development of new tissue, the elaborated sap of Plants supplies the materials for the production of that immense variety of organic compounds, in which the Vegetable World is so rich; compounds whose use in the economy of the Plant is frequently by no means apparent, but whose value to the Animal Creation and to Man would frequently appear to be the sole end of their preparation. These compounds are frequently designated as Vegetable *Secretions;* but this term cannot be applied to them, in the sense in which it is used in Animal physiology. For all these products are contained and stored-up in cells, which continue to form part of the organised fabric, instead of being cast-forth from it (§ 398); and they might rather be compared to the fat of animals, which is in like manner separated from the blood by the development of adipose cells, that constitute permanent components of the organism. Now of the cause of the immense variety of these products that presents itself in different plants, and even in different parts of the same plant,—the fixed and volatile oils, resins, gums, colouring matters, alkaloids, acids, &c., &c.,—no other account can be given, than that each component cell generates its own peculiar products, at the expense of the nutrient materials supplied to all alike, just as, among the Unicellular Plants, each species may form a distinct organic compound. Thus, to take a simple case, in the petal of a *Heartsease* or any similar particoloured flower, one cell forms purple-colouring matter, while another in close proximity with it forms red-colouring matter; just as *Protococci* and

Hæmatococci, growing under the same circumstances, and at the expense of the same inorganic compounds, respectively, generate *green* and *blood-red* endochrome. There are, however, certain chemical relations between these compounds, which become of peculiar interest when taken in connection with the fact, that the process by which the Plant generates them all out of the water, carbonic acid and ammonia which supply their materials, is essentially one of *deoxidation;* of these relations a general account will now be given.

(I.) Commencing with the Non-azotized compounds, which may be regarded as formed at the expense of water and carbonic acid alone, we find that the substances in whose production least oxygen would have to be set free, are the stronger *Vegetable Acids*, in which the oxygen exceeds the hydrogen.

	Formula.	Carb. acid used.	Water used.	Oxygen separated.
Oxalic Acid (dry) .	$C_2\ H\ O_4$	2 equiv.	1 equiv.	1 equiv.
Gallic Acid . . .	$C_7\ H_3\ O_5$	7 ,,	3 ,,	12 ,,
Tartaric Acid . . .	$C_8\ H_6\ O_{12}$	8 ,,	6 ,,	10 ,,
Malic Acid . . .	$C_8\ H_6\ O_{10}$	8 ,,	6 ,,	12 ,,
Citric Acid . . .	$C_{12}\ H_8\ O_{14}$	12 ,,	8 ,,	18 ,,
Tannic Acid . . .	$C_{18}\ H_8\ O_{12}$	18 ,,	8 ,,	32 ,,

(II.) The next group is formed by the indifferent *Neutral Compounds*, which take the largest share in the vegetative operations. These invariably contain hydrogen and oxygen in the proportion to form water; so that they may be theoretically considered as formed of carbon + water, the whole of the oxygen of the carbonic acid being separated, but none of that of the water.

	Formula.	Carb. acid used.	Water used.	Oxygen separated.
Cellulose	$C_{12}\ H_{10}\ O_{10}$	12 equiv.	10 equiv.	24 equiv.
Starch	$C_{12}\ H_{10}\ O_{10}$	12 ,,	10 ,,	24 ,,
Cane-sugar . . .	$C_{12}\ H_{11}\ O_{11}$	12 ,,	11 ,,	24 ,,
Gum	$C_{12}\ H_{11}\ O_{11}$	12 ,,	11 ,,	24 ,,
Grape-sugar (dry) .	$C_{12}\ H_{12}\ O_{12}$	12 ,,	12 ,,	24 ,,

(III.) A third group consists of those *neutral* bodies,—chiefly *bitter, acrid, coloured,* or yielding colours with ammonia,—in which not only the oxygen of the carbonic acid has been separated, but also a part of that which forms water. Such bodies are very numerous, as well as very various in their characters: the following are among the most diversified examples; the first being nearly allied to sugar, the second an acrid poison, the third a pure bitter, the fourth a gelatinising substance, and the fifth a coloured body.

	Formula.	Carb. acid used.	Water used.	Oxygen separated.
Mannite	$C_6\ H_7\ O_6$	6 equiv.	7 equiv.	13 equiv.
Elaterine	$C_{20}\ H_{14}\ O_5$	20 ,,	14 ,,	49 ,,
Salicine	$C_{26}\ H_{18}\ O_{14}$	26 ,,	18 ,,	56 ,,
Pectine	$C_{28}\ H_{20}\ O_{26}$	28 ,,	20 ,,	50 ,,
Hæmatoxyline . .	$C_{40}\ H_{17}\ O_{13}$	40 ,,	17 ,,	84 ,,

(IV.) From these we pass to the *Oxygenated Volatile Oils*, and the *Volatile Acids* related to them; the latter being formed from the former by simple oxidation, and approaching the resins in composition. A few instances will suffice.

	Formula.	Carb. acid used.	Water used.	Oxygen separated.
Oil of Bitter Almonds	$C_{14} H_6 O_2$	14 equiv.	6 equiv.	32 equiv.
Benzoic Acid . .	$C_{14} H_6 O_4$	14 ,,	6 ,,	30 ,,
Oil of Spiræa . .	$C_{14} H_6 O_4$	14 ,,	6 ,,	30 ,,
Salicylic Acid . .	$C_{14} H_6 O_6$	14 ,,	6 ,,	28 ,,
Oil of Anise . . .	$C_{16} H_8 O_4$	16 ,,	8 ,,	36 ,,
Anisic Acid . . .	$C_{16} H_8 O_6$	16 ,,	8 ,,	34 ,,
Oil of Cinnamon .	$C_{18} H_8 O_2$	18 ,,	8 ,,	42 ,,
Cinnamic Acid . .	$C_{18} H_8 O_4$	18 ,,	8 ,,	40 ,,

(v.) Another group is formed by the *Volatile Oily* and *Fatty Acids,* together with certain bases with which they are ordinarily found in combination,—as glycerine and the oxides of ethyle, amyle, &c.,—such compounds being the sources of the flavour of many fruits.

	Formula.	Carb. acid used.	Water used.	Oxygen separated.
Oxide of Ethyle . .	$C_4 H_5 O$	4 equiv.	5 equiv.	12 equiv.
Glycerine	$C_6 H_4 O_2$	6 ,,	4 ,,	14 ,,
Butyric Acid . . .	$C_8 H_8 O_4$	8 ,,	8 ,,	20 ,,
Valerianic Acid . .	$C_{10} H_{10} O_4$	10 ,,	10 ,,	26 ,,
Oxide of Amyle . .	$C_{10} H_{11} O$	10 ,,	11 ,,	30 ,,
Capric Acid . . .	$C_{20} H_{20} O_4$	20 ,,	20 ,,	56 ,,
Margaric and Stearic Acids	$C_{34} H_{34} O_4$	34 ,,	34 ,,	98 ,,

(vi.) The next group includes a large number of isomeric and polymeric *Resins* and *Resinous Acids,* in which little oxygen is left; notwithstanding their great varieties in character, there is a remarkable uniformity in composition among them.

	Formula.	Carb. acid used.	Water used.	Oxygen separated.
Many Resins . . .	$C_{10} H_7 O$	10 equiv.	7 equiv.	26 equiv.
Camphor	$C_{10} H_8 O$	10 ,,	8 ,,	27 ,,
Borneo Camphor . .	$C_{20} H_{18} O_2$	20 ,,	18 ,,	56 ,,
Many Resins . . .	$C_{20} H_{14} O_2$	20 ,,	14 ,,	52 ,,
Many Resinous Acids	$C_{20} H_{15} O_2$	20 ,,	15 ,,	53 ,,

(vii.) The last group consists of the *Carbo-hydrogens,* in which the whole of the oxygen, both of the carbonic acid and of the water, has been separated, so that no further deoxidation can take place. Hence these compounds are very permanent, and are chiefly altered by their natural tendency to *absorb oxygen* under favourable circumstances.

	Formula.	Carb. acid used.	Water used.	Oxygen separated.
Oil of Lemons, &c. . .	$C_5 H_4$	5 equiv.	4 equiv.	14 equiv.
Oil of Turpentine, &c. .	$C_{10} H_8$	10 ,,	8 ,,	28 ,,
Oil of Juniper, &c. . .	$C_{15} H_{12}$	15 ,,	12 ,,	42 ,,

360. It is supposed by Liebig, that oxalic acid, which approaches the nearest of all these organic compounds, as regards both its composition and its properties, to the inorganic bodies which furnish its components, is that which is first formed, and the other acids from it; then sugar, starch, &c., from the acids; bitter, acrid, and coloured compounds from sugar, starch, &c.; then oxygenated volatile oils, then the oily and fatty acids, either from the preceding volatile oils or from sugar; then the resins, from fats or from sugar; and lastly the carbo-hydrogens. And this view seems favoured by the very extensive diffusion of these acids, which, though found in large quantities only in certain plants, may be detected

in small quantities in a great variety (§ 202). It is open, however, to too many objections, to admit of being received as more than an ingenious hypothesis.* Many of the substances of the same or even of different groups may be converted, by simply chemical processes, one into another. Thus the neutral bitter, Salicine, is convertible by simple oxidation (effected by means of the action of dilute sulphuric acid on bichromate of potass mingled in its solution) into the fragrant Oil of Spiræa and Grape-sugar; this change being expressed in the following formula :—

$$\left.\begin{array}{lrrr} & \text{C.} & \text{H.} & \text{O.} \\ \text{1 Equiv. Salicine .} & 26 & 18 & 14 \\ \text{2 ,, Oxygen .} & 0 & 0 & 2 \\ \hline & 26 & 18 & 16 \end{array}\right\} = \left\{\begin{array}{rrrl} \text{C.} & \text{H.} & \text{O.} & \\ 14 & 6 & 4 & \text{1 equiv. Oil of Spiræa.} \\ 12 & 12 & 12 & \text{1 equiv. Grape-sugar.} \\ \hline 26 & 18 & 16 & \end{array}\right.$$

So from the Hydrated Oxide of Amyle (an oil-like body, which is produced during the distillation of alcohol from fermented grain or potatoes), the pungent fœtid Valerianic acid may be obtained, by treating it with hydrate of potass, which occasions the disengagement of two equivalents of hydrogen, and the absorption of two of oxygen from the atmosphere, as follows :—

	C.	H.	O.	
1 equiv. Hydrated Oxide of Amyle .	10	12	2	
2 equiv. of Oxygen added	0	0	2	
2 equiv. Hydr. subtracted	0	— 2	0	
	10	10	4	= 1 equiv. Valerianic acid.

It will be observed that in both these transformations *oxygen is absorbed;* and there can be no doubt that this will be frequently the case, although the great bulk of the changes which take place in the act of vegetation are of the opposite character. In fact, it is much easier to *oxidise*, than to *deoxidise* Organic Compounds, by the processes of ordinary Chemistry; and there are several among the foregoing, in which simple exposure to air will produce this effect. The carbo-hydrogens and the essential oils, for example, are rapidly converted into resins, unless carefully secluded from oxygen; the red colours of leaves and flowers are produced from the yellow or the blue by oxygenation; and there are many plants with fleshy leaves, which form acids by an oxidating process during the night, these being again decomposed by day.

361. The mode of formation of those Azotized compounds, which differ from the preceding, not only in the presence of an additional element, but also in the far greater complexity of their atomic composition, cannot be so readily conceived; yet there are certain links of connection between these and the non-azotized, which indicate that the agency whereby they are produced is of the same general nature. Thus, if we direct our attention in the first instance to the azotized substances which contain neither sulphur nor phosphorus, and whose atomic composition is comparatively simple, we find that they may be conceived to be formed by a process of *deoxidation*, out of a certain number of equivalents of carbonic acid, water, and ammonia; as in the following examples :—

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* "Familiar Letters on Chemistry," 3rd edit., pp. 177, 178.

	Formula.	Carb. Acid used.	Water used.	Amm. used.	Oxygen separ.
Asparagine	$C_8\ N_2\ H_{10}\ O_8$	8	4	2	12
Amygdaline	$C_{40}\ N\ H_{27}\ O_{22}$	40	24	1	82
Nicotine .	$C_{10}\ N\ H_8$	10	8	1	28
Morphine	$C_{35}\ N\ H_{20}\ O_6$	35	17	1	81
Quinine .	$C_{20}\ N\ H_{12}\ O_6$	20	9	1	43
Strychnine	$C_{44}\ N_2\ H_{22}\ O_4$	44	16	2	106
Furfurine	$C_{30}\ N_2\ H_{12}\ O_6$	30	6	2	60

Now the first of these substances (also termed *Malamide*), which occurs abundantly in Asparagus and in the Mallow, but which is also found in germinating seeds and etiolated plants, may be formed artificially from neutral malate of ammonia (malic acid + 2 ammonia + 2 water) by depriving it of two equivalents of its water of crystallisation, as thus :—

$$\underbrace{C_8\ H_4\ O_8,\ 2\ NH_3,\ 2\ HO}_{\text{Malate of Ammonia.}} = \underbrace{C_8\ N_2\ H_{10}\ O_8}_{\text{Malamide.}} + 2\ HO$$

This is an example of the class of bodies termed *amides*, which are formed by the elimination of two equivalents of water from neutral or acid salts consisting of ammonia in union with organic acids, and which seem to perform a very important part in Organic Chemistry.—The last of these substances, on the other hand, is at present known only as an artificial product; yet its relations are so close to the vegetable alkaloids, that it can scarcely be doubted that they are generated in a manner essentially the same. When bran is treated with sulphuric acid, an oily substance termed *furfurol,* whose formula is $C_{15}\ H_6\ O_6$ may be distilled over; and when this is brought into contact with ammonia, it forms a *neutral* crystalline compound *furfurolamide,* three equivalents of water being parted-with, as thus :—

$$\underbrace{C_{15}H_6O_6}_{\text{Furfurol.}} + NH_3 = \underbrace{C_{15}\ H_6\ NO_3}_{\text{Furfurolamide.}} + 3\ HO.$$

Now when furfurolamide is dissolved in hot potash, it is transformed, without any other change of composition than the coalescence of two of its atoms into one (the atomic equivalents of furfurine being exactly double those of furfurolamide), into the *basic* substance *furfurine,* which approaches nearly to several vegetable alkaloids in its general characters, and has the bitter taste of quinine, with some measure also (it is asserted) of its medicinal powers. It is peculiarly interesting to remark, that in this last transformation (as in the like transformation of 3 equivalents of Oil of Bitter Almonds + 2 Ammonia into 1 Hydrobenzamide + 6 Water, and in the metamorphosis of this neutral Hydrobenzamide, by boiling in caustic potash, into the powerful organic base Amarine), there is an approach to that wonderful process of building-up complex atoms or molecules from such as are less complex, which the Chemist had previously found beyond his powers—such artificial transformations as he could effect, having consisted in the resolution or breaking-up of the complex natural compounds into others more simple.

362. Hence, then, we are naturally led to believe, that the production of those most complex Azotized compounds, into which Sulphur also enters in definite proportions, and for which the presence of Phosphorus also is necessary (though it is not yet certain whether it is required as a *mate-*

rial constituent, or whether its *influence* only is needed), is accomplished by agencies of a nature similar to those which are operative in the preceding cases. The very smallest number of equivalents whose presence is indicated by analysis in a molecule of *Vegetable Albumen*, is 216 Carbon, 169 Hydrogen, 27 Nitrogen, 2 Sulphur, 68 Oxygen. This formula may be deduced either from the inorganic compounds already mentioned, with the addition of sulphuric acid, or from the formula of sugar, with ammonia and sulphuric acid; oxygen alone being expelled in the first case, and oxygen and water in the second. Thus:—

$$\overset{\text{Carb. Acid}}{216} + \overset{\text{Water.}}{88} + \overset{\text{Amm.}}{27} + \overset{\text{Sulph. Acid.}}{2} = \overbrace{C_{216}H_{169}N_{27}S_2O_{68}}^{\text{Albumen.}} + \overset{\text{Oxygen.}}{458}$$

Or, supposing sugar to be first formed;—

$$\overset{\text{Carb. acid.}}{216} + \overset{\text{Water.}}{216} = \overset{\text{Sugar.}}{18\ (C_{12}\,H_{12}\,O_{12})} + \overset{\text{Oxygen.}}{432}$$

$$\overset{\text{Sugar.}}{18\ (C_{12}\,H_{12}\,O_{12})} + \overset{\text{Amm.}}{27} + \overset{\text{Sulph. Ac.}}{2} = \overbrace{C_{216}H_{169}N_{27}S_2O_{68}}^{\text{Albumen.}} + \overset{\text{Water.}}{128} + \overset{\text{Oxygen.}}{26}$$

Thus we perceive that in these higher and more recondite changes, as in those lower operations which fall more readily within our comprehension, the power of *deoxidation* which the vegetable cell has such a remarkable power of exerting, is intimately allied with the *building-up of complex atoms;* and in proportion as Chemists find themselves able to imitate the Vegetable processes, instead of being restricted to the coarser methods of the ordinary laboratory, will they probably succeed in elaborating the same *chemical* products; although Vitality alone can impress upon them those peculiar characters, which prepare them for being appropriated as materials for the construction of the organised fabric.

363. Thus, then, as has been well remarked by Prof. Gregory,* we see, that "Vegetables cannot possibly grow and form seeds, without at the same time producing, as parts of their constructure, the food of Animals in its two great forms; non-nitrogenous and respiratory food, namely, starch, sugar, gum, and oils; and nitrogenous, plastic, and sanguigenous food, namely, albumen, fibrin, and casein. The former, which do not enter into the formation of blood,—save, to a small extent, oils or fats,—may exist free from ashes or mineral matter, although these are necessary to their production; but the latter cannot exist without containing (at all events) phosphates. And thus, by the beautiful arrangement which renders albumen, fibrin, and casein indispensable to the development of plants, and to the production even of starch, sugar, and fat; and which has rendered the presence of phosphates indispensable to the existence of albumen, fibrin, and casein; vegetables cannot grow, nor produce the plastic food of animals, or that which yields blood, without at the same time supplying to animals the earthy matter required for their bones, and, in a smaller proportion, for the blood and all the tissues. If albumen, &c., could be formed without phosphates, or even if blood and muscle could exist without phosphates, still animals could not exist or be formed with-

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* "Handbook of Organic Chemistry," p. 483.—It is chiefly from the excellent section of that treatise, 'The Nutrition of Plants and Animals,' that the materials of the four preceding paragraphs have been derived.

out bone-earth. As it has been arranged with perfect wisdom, however, the mere fact that a Plant has grown, necessarily implies that it contains the materials required to support animal life; provided, of course, it be not a poisonous plant, though probably there is no plant which may not serve as food for some animal."

364. There is one of the above-named organic compounds, which is so peculiarly related to the vital operations of the economy, as to require special notice. This is *Starch*, a substance very universally diffused through the Vegetable kingdom. When removed from the plant, Starch exists in the form of minute granules, presenting great diversities of figure and dimension; but having, for the most part, a limit of size, and a characteristic aspect, in each tribe of plants, by which its source may frequently be determined. Each granule, when examined by the microscope, is seen to be marked by numerous lines, usually having more or less of a concentric arrangement; and by the use of re-agents, it may be shown to have a vesicular character, the lines just mentioned being the result of plaitings or foldings which the wall of the vesicle has undergone.* Several such granules, of different sizes, are usually found within one cell; and it seems probable that they are formed by successive additions to their substance, by imbibition through the outer layer of the vesicle; since the interior is occupied by matter of more fluid consistence. When exposed to the heat of about 160°, the starch-grain bursts, and the inner layers are readily dissolved by water; and this is the explanation of the fact, that starch once dissolved in hot water can never be restored to its original form. In composition, starch is very closely related to gum and cellulose; and it may, in fact, be regarded as a store of nutritive matter, which has undergone such an alteration that it can be kept apart from the surrounding juices, and can thus be reserved for some special purpose. Thus, we find it stored-up in the *seeds* of most species, either forming a separate 'albumen,' as in the Grasses, or taken into the structure of the embryo, and constituting the mass of the fleshy cotyledons, as in the Leguminosæ, &c.; in each of these cases it serves as a magazine of food for the nutrition of the embryo, previously to the development of those organs which enable it to maintain an independent existence. Similar reservoirs are occasionally formed by the enlargement of the *stem* into tubers, for the nutrition of the buds to be developed from them, as in the Potato, Arrow-root-plant, &c.; or by the accumulation of the same material in fleshy *roots*, *bulbs*, &c., from which stems rapidly grow-up. Starch is also found abundantly in the soft interior (improperly called pith) of the stem of the Sago-Palm and other Monocotyledons, where it seems destined to assist the evolution of the young leaves; and in the fleshy expansions of the flower-stalk (termed *receptacles*); on which, in many orders, the flower is situated, and in which it seems to answer a corresponding purpose.

365. In all these cases, the immediate end of the accumulation of Starch is, that it may be ready for the nutrition of the growing body before this is capable of obtaining food for itself; and it may be observed that the deposit continues to increase as long as the plant is in active vegetation,—arrives at its maximum,—and then, remaining stationary during the winter, begins to decrease in the spring. The deposition of

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* See Busk 'On the Structure of the Starch-Granule,' in "Transact. of Microsc. Soc.," New Series, Vol. I. p. 58.

Starch fulfils, therefore, an obvious purpose in the Vegetable economy; but we cannot doubt the wise and benevolent intention of the Creator, in thus providing a store of nutritious and palatable food for Man, in situations whence he can so easily obtain it; and it is interesting to remark that, as it almost always exists in an insulated form, it may be obtained in a state of purity from many vegetables which would otherwise be very poisonous. Before it can be applied to the nutrition of the plant, however, its condition must be altered. Thus, in the germination of seeds, it is converted into sugar; the same change takes place in the tuber of the potato, during the evolution of its buds; and during the period of flowering, the starch previously deposited in the receptacle undergoes a similar transformation (§ 274). This conversion is a process which the Chemist can imitate; for if the fecula be first heated, so that its vesicles are ruptured, and it be then treated with dilute sulphuric acid, it is converted into sugar; and the salivary matter of animals possesses the same converting power in a remarkable degree (§ 163). The change is effected in the Vegetable economy by the operation of an azotized secretion called *diastase;* which seems to be formed for the express purpose, and which may be obtained in a separate state, either from malt, or from the neighbourhood of the 'eyes' or buds of the potato, producing the same effects in the laboratory of the Chemist, as in the Vegetable economy. Its operation is really that of a 'ferment;' for the conversion of starch into sugar is dependent upon an incipient decomposition of the diastase, which, when it proceeds further, excites the alcoholic fermentation in the saccharine product. And the liberation of carbonic acid appears due to the necessity for getting-rid of the excessive proportion which the carbon of starch bears to its oxygen and hydrogen, as compared with that which exists in sugar. For

$$\begin{array}{ll} \text{12 equiv. Starch} & = C_{144}\,H_{120}\,O_{120} \\ \text{10 equiv. Grape-sugar} & = C_{120}\,H_{120}\,O_{120} \\ \hline \text{Excess of Carbon in Starch} \quad . & \quad 24 \end{array}$$

An extrication of carbonic acid seems to take place wherever this metamorphosis occurs (§ 274); and it is probable that the secretion of diastase is equally general.

3. *Nutrition in Animals.*

366. In tracing the gradual incorporation of the alimentary materials ingested by Animals, into their organised fabric, it will be convenient to give our first attention to the cases in which so wide an interval exists between the points at which nutriment is absorbed and those at which it is appropriated, that we are able to trace a gradual metamorphosis in the components of the nutritive fluid, whereby it is *assimilated* in nature to the tissues, whose *formative* operations are performed at its expense. The nutritive materials prepared by the Digestive process, are taken into the circulation of Vertebrated animals, as already shown (CHAP. IV.), through two distinct channels, the Blood-vessels and the Absorbents. Now all the veins which are formed by the reunion of the capillaries of the gastro-intestinal canal, converge into the *Vena Portæ,* which, like an artery, distributes the blood, thus charged with crude materials, to the secreting apparatus of the Liver. It was formerly

supposed that the agency of that gland was limited to the elimination, from the blood subjected to its influence, of the materials of the biliary secretion; but there is now ample evidence that the blood itself is changed by its means, in a manner that indicates an *assimilating,* as well as a *depurating* action. One of the most important of these changes, is the assimilation of that crude *albuminous* product, recently distinguished as 'albuminose,' which is formed by the solution of albumen, fibrin, casein, &c., in the alimentary canal. This product, as was long since remarked by Dr. Prout,[*] is deficient in some of the most characteristic properties of true Albumen; for it is scarcely coagulated either by heat or by nitric acid, and it freely transudes through organic membranes which entirely check the passage of the latter. It is found abundantly in the blood of the mesenteric vein during digestion, whilst it does not present itself in that of the hepatic vein; so that we may infer that it is converted into true blood-albumen in its passage through the liver. That an assimilating power is exerted by the Liver on albuminous substances, is further indicated by the fact ascertained by M. Cl. Bernard, that if a solution of egg-albumen' be injected into any part of the systemic circulation, albumen speedily makes its appearance (like other soluble substances which are foreign to the body) in the urine; but that if the same substance be injected into the vena portæ, it does not show itself in the urine, being apparently incorporated with the blood by the agency of the liver. It is now certain, too, that the liver elaborates from some other constituents of the blood a *saccharine* compound (liver-sugar), which is destined for immediate elimination by the lungs, and which, being much more readily carried-off by the respiratory process than either grape-sugar or cane-sugar, may be regarded as its most appropriate pabulum.[†] Moreover the liver converts grape-sugar and cane-sugar—absorbed by the tributaries of the vena portæ, and brought to it by the blood-current —into the form of 'liver-sugar,' of whose presence the blood is much more tolerant; for whilst the injection of a small quantity of cane-sugar into the general circulation renders the urine saccharine, no less than 240 times as much liver-sugar may be thus introduced without producing the same effect; whilst if the cane-sugar be injected into the vena portæ, so much larger a quantity may be introduced without making the urine saccharine, that it must obviously have been converted in passing through the liver.[‡] Further, it appears from M. Bernard's researches, that *fatty matters* are elaborated in the liver, from saccharine or some other constituents of the blood; so that even when no fat can be detected in the blood of the vena portæ, that of the hepatic vein may contain a considerable amount of it. A portion of this fat may be destined to immediate elimination in the lungs; but if the supply that should be introduced by the lacteals be deficient, it would doubtless be made subservient to the formative processes. Lastly, it has been observed by Prof. E. H. Weber, that during the last three days of incubation of the chick, the liver is made bright-yellow by the absorption of the yolk, which fills and clogs all the minute branches of the portal veins; and that in time, the materials of the yolk disappear, part being developed into *blood-corpuscles* and other constituents of blood, which enter the circulation, and the rest forming bile, and being discharged into the intestines.* There is no evidence, however, that blood-corpuscles are thus generated in the liver during later life.—Thus we may look upon the Liver as an *assimilating organ* of very comprehensive endowments; being the seat of the elaboration of albumen, of the generation of fatty matter, and (under certain circumstances at least) of the production of red-corpuscles, which are three of the most important elements in the preparative stages of the nutrient process; and being further capable of preparing the blood most advantageously for the function next in importance, the generation of heat.

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[*] "Bridgwater Treatise," 3rd edit., p. 444.

[†] See the Lectures of M. Cl. Bernard on the 'Functions of the Liver,' delivered before the Collége de France, and published in "L'Union Médicale" for 1850; and his Memoir entitled "Nouvelle Fonction du Foie, considéré comme Organe Producteur de Matière Sucrée chez l'Homme et chez les Animaux," 1853.

[‡] See Magendie in "L'Union Médicale" for 1849, Nos. 72, 75, 79.

367. We have now to enquire what are the changes which the *Chyle* absorbed into the *Lacteal* system undergoes, during its progress from the walls of the intestines to the Thoracic Duct. The fluid drawn from the lacteals that traverse the intestinal walls, has no power of spontaneous coagulation; whence we may infer that it contains little or no fibrin. It contains albumen in a state of complete solution, as we may ascertain by the influence of heat or acids in producing coagulation. And it includes a quantity of fatty matter, which is not dissolved, but is suspended in the form of globules of variable size. The quantity of this evidently varies with the character of the food; it is more abundant, for instance, in the chyle of Man and of the Carnivora, than in that of the Herbivora. It was formerly supposed that the milky colour of the chyle is owing entirely to its oil-globules; but Mr. Gulliver has pointed out that it is really due to an immense multitude of far more minute particles, which he has described under the name of the *molecular base* of the chyle. These molecules are most abundant in rich, milky, opaque chyle; whilst in poorer chyle, which is semi-transparent, the particles float separately, and often exhibit the vivid motions common to the finely-divided molecules of various substances. Such is their minuteness, that, even with the best instruments, it is impossible to determine either their form or their dimensions with exactness; they seem, however, to be generally spherical; and their diameter may be estimated at between 1-36,000th and 1-24,000th of an inch. As they are readily soluble in ether, there would seem to be no doubt of their oleaginous nature; but it appears probable that each of them is surrounded with that thin membranoid film, which, as first pointed out by Ascherson, is formed whenever oily and albuminous matters are brought into contact. —No other particles than these are observable in the chyle drawn from the lacteals near the villi; but after the fluid has passed through the Mesenteric glands, it exhibits very marked changes. The presence of fibrin (which must have been formed at the expense of the albumen) now begins to declare itself, by the spontaneous coagulation of the fluid; the quantity of molecules and larger oily particles diminishes, perhaps by their passage into the blood when the two fluids are brought into close relation in the mesenteric glands; and a set of peculiar floating cells or

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* Henle and Pfeufer's "Zeitschrift," 1846.

'chyle-corpuscles' now for the first time make their appearance. The average diameter of these is about 1-4600th of an inch; but they vary from about 1-7000th to 1-2600th,—that is, from a diameter about half that of the human blood-corpuscles, to a size about a third larger. This variation probably depends in great part upon the period of their growth. They are usually minutely granulated on the surface, seldom exhibiting any regular nuclei, even when treated with acetic acid; but three or four central particles may sometimes be distinguished in the larger ones. These corpuscles are particularly abundant in the chyle obtained by puncturing the mesenteric glands themselves; and it would seem not improbable, that they are identical with the spherical nucleated particles, which are so copiously developed within the dilated lacteal tubes in their course through those bodies (§ 184). The glandular character of these cells, and their continued presence in the circulating fluid, seem to indicate that they have an important concern in the process of Assimilation. It is only in the Chyle which is drawn from the lacteals intervening between the mesenteric glands and the receptaculum chyli, that the spontaneous coagulability of the fluid is so complete, as to produce a perfect separation into *clot* and *serum*. The former is a consistent mass, which, when examined with the microscope, is found to include many of the chyle-corpuscles, each of them surrounded with a delicate film of oil; the latter bears a close resemblance to the serum of the blood, but has some of the chyle-corpuscles suspended in it. Considerable differences present themselves, however, both in the perfection of the coagulation, and in its duration. Sometimes the chyle sets into a jelly-like mass; which without any separation into coagulum and serum, liquefies again at the end of half an hour, and remains in this state. The coagulation is usually most complete in the fluid drawn from the receptaculum chyli and thoracic duct; and here the resemblance between its floating cells, and the white or colourless corpuscles of the blood, becomes very striking.

368. The *Lymph*, or fluid of the *Lymphatics*, sensibly differs from the Chyle in its comparative transparency; its want of the opacity or opalescence which is characteristic of the latter, being due to the absence, not merely of oil-globules, but also of the 'molecular base.' It contains floating cells, which bear a close resemblance to those of the Chyle on the one hand, and to the colourless corpuscles of the Blood on the other; and these, as in the preceding case, are most numerous in the fluid which is drawn from the lymphatics that have passed through the glands, and in that obtained from the glands themselves. Lymph coagulates like chyle; a colourless clot being formed, which encloses the greater part of the corpuscles. The chief chemical difference between the Chyle and the Lymph, consists in the much smaller proportion of solid matter in the latter, and in the almost entire absence of fat, which is an important constituent of the former. This is well shown in the following comparative analyses, performed by Dr. G. O. Rees,* of the fluids obtained from the Lacteal and the Lymphatic vessels of a donkey, previously to their entrance into the thoracic duct; the animal having had a full meal seven hours before its death.

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* "Medical Gazette," Jan. 1, 1841.

	Chyle.	*Lymph.*
Water	90·237	96·536
Albuminous matter (coagulable by heat)	3·516	1·200
Fibrinous matter (spontaneously coagulable)	0·370	0·120
Animal extractive matter, soluble in water and alcohol	0·332	0·240
Animal extractive matter, soluble in water only	1·233	1·319
Fatty matter	3·601	a trace.
Salts ;—Alkaline chloride, sulphate, and carbonate, with traces of alkaline phosphate, oxide of iron	0·711	0·585
	100·000	100·000

The Lacteals may be regarded as the Lymphatics of the intestinal walls and mesentery; for the fluid which they contain during the intervals of digestion, is in all respects conformable to the lymph of the lymphatic trunks.

369. Thus by the admixture of the aliment newly-introduced from without, with the matter which has been taken-up in the various parts of the system, and by the elaboration which these undergo in their course towards the Thoracic Duct, a fluid is prepared, which bears a strong resemblance to Blood in every particular, save the presence of *red* corpuscles. Even these, in a state of incipient development, may sometimes be found in the contents of the thoracic duct, in sufficient amount to communicate to them a perceptibly reddish tinge. The fluid of the thoracic duct may be compared to the blood of Invertebrated animals; from which the red corpuscles are almost or altogether absent, but which contains white or colourless corpuscles; and whose coagulating power is comparatively slight, in consequence of its small proportion of fibrin. And we hence see, why these animals should require no *special* absorbent system; since the blood-vessels convey a fluid, which is itself so analogous to the chyle and lymph to be absorbed, that the latter may be at once introduced into it, without injuring its qualities. The elaboration of this fluid in the Vertebrata would seem most probably due to the assimilating agency of the cells contained within the absorbent glandulæ, and of those which float in it during its passage through the vessels; and we may, in fact, regard the whole of the special Absorbent system in the light of an assimilating apparatus, fitted not merely to take-up, but also to prepare for admission into the circulating fluid, such appropriate materials as may be presented to it in the requisite condition. One important part of this preparation, in the case of the Lacteals, seems to consist in the intimate incorporation of *fatty* particles with *albuminous* substances. Oily matter, as we have seen, is a constituent of the food of nearly all animals; and where it does not exist as such in the food, it is generated in the system at the expense of farinaceous compounds; and since this takes place in cold- as well as warm-blooded animals, it is obvious that the oleaginous particles must have some special purpose in the system, altogether irrespective of the maintenance of the combustive process. Further, we have seen that one of the chief peculiarities of the Chyle consists in the peculiar state in which these fatty particles are found; and this state corresponds so closely with that in which we find them dispersed as 'molecules' through the solids and fluids of the body, that we can scarcely hesitate in attributing to it some peculiar relation to the nutritive operations. Of the nature of this relation we obtain

some further indication from the fact, that oleaginous particles may be constantly distinguished in the nuclei or cytoblasts of growing cells or fibres, as well as in the nuclear bodies scattered through an 'organisable blastema;' so that it may be affirmed with much probability, that the presence of fatty matter is not less essential to the formative operations, than is that of the albuminous compounds themselves.*

370. There can be little doubt that we are to rank among the assimilating organs, certain bodies, known as 'Vascular Glands' or 'Glands without Ducts,' which are found in Vertebrated animals, in intimate relation with various parts of the sanguiferous system. These are, the *Spleen*, the *Thymus Gland*, the *Thyroid Gland*, the *Supra-Renal Capsules*, the *Glandulæ Solitariæ*, and *Peyerian glandulæ* of the walls of the Intestinal canal, and some smaller bodies elsewhere. Many points in the structure of these organs, especially of the one first-named, are still far from being satisfactorily made out; and of their function it would be rash to speak too confidently. Nevertheless it may be said of them all, that when in most active operation, they are largely supplied with blood, and that they are made up for the most part of a parenchyma, which is usually contained in isolated vesicles, though in the Thymus this occupies one large branching cavity. These vesicles, however, do not seem to be analogous to those of ordinary glands, which are really dilated cells, giving origin to successive broods of secondary cells in their interior (§ 401); for they have no proper limitary membrane, and seem rather to be formed by the partial coalescence of the elements of the surrounding tissue, for the isolation of their parenchymatous contents, which consist of nuclei and cells, in various stages of development, imbedded in a *blastema* or formative fluid. The vesicles are traversed by blood-vessels, which sometimes form a minute capillary network, whilst in other instances their arrangement is rather penicillate (brush-like), the arterial twig subdividing into a tuft of ramuscules, which reunite again after passing separately through the parenchyma. The primary form of these bodies is the 'solitary gland' of the intestinal canal; "which," as Mr. Huxley remarks, "is nothing but a local hypertrophy of the indifferent element of the connective tissue of the part, and possesses no other capsule than that which necessarily results from its being surrounded by the latter. A number of such bodies as these, in contiguity, constitute, if they be developed within a mucous membrane, a Peyer's patch; if within the walls of the splenic artery and its ramifications, a Spleen; if within the walls of lymphatics, a Lymphatic gland; if in the neighbourhood or within the substance (as in Fishes) of a kidney, a Supra-Renal body; if in relation with a part of the brain, a Pituitary body."† It can scarcely be ques-

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* This view derives strong confirmation from the very remarkable effect of Cod-liver oil in improving the nutrition of Tubercular subjects; and from the curious prophylactic influence of the oleaginous diet of the Icelanders, a people whose habits are such as would peculiarly favour the development of Scrofula, but who are most remarkably free from any form of it. The importance of oleaginous matter to the process of textural nutrition, and the probable *rationale* of the beneficial effects of Cod-liver oil (which may be regarded as by far the most important among the recent improvements in Medical practice), were first developed, the Author believes, by his friend Prof. J. H. Bennett, in his treatise on Cod-Liver Oil, published in 1841.

† 'On the Malpighian Bodies of the Spleen,' &c., in "Microscopical Transactions," New Series, p. 81.

tioned that these bodies take a share in the function of Assimilation; elaborating the nutrient materials which are brought to them, and restoring them again in a more elevated condition. Most of them exert this action upon the blood; but from the special relation to the Absorbent system, which the researches of Brucke have shown the Peyerian bodies to possess, it seems probable that they belong to the same category with the Absorbent glandulæ, and exercise their office chiefly upon the chyle. The Thymus, again, which has a large cavity for the reception of fluid, probably withdraws for a time the materials upon which it exercises its transforming power, and serves to store them until they may be required.—This view of their action is strongly confirmed by the fact, that the greatest activity of the Thymus and Thyroid bodies, and of the Supra-Renal capsules, is during fœtal life and early infancy, when the formative processes are being performed with extraordinary energy, and are making a large demand upon the assimilative powers; and it has been further shown by Prof. Goodsir, that these three organs may be regarded as involuted portions of the 'germinal membrane,' which is the first assimilating organ possessed by the fœtus (CHAP. XI.), and are in absolute continuity with each other at an early period of fœtal life.*

371. There is no improbability, however, in the idea that these organs may severally have some subsidiary or supplementary function to perform, varying according to their respective structure, position, and connections. Thus it has been observed by Mr. Simon, that the Thymus of hybernating Mammalia, instead of dwindling-away (as in other instances) when full growth has been attained, greatly enlarges and becomes laden with fat, this accumulation taking place especially at the approach of winter; so that the organ, after it has ceased to perform its original function, is then used as a sort of storehouse for combustive material.—The Spleen, which has a different origin from the other three, would appear to serve, through the extraordinary distensibility of its vessels, as a kind of *diverticulum*, to relieve the vessels of the digestive viscera, when they are compressed by undue accumulation of the contents of their cavities, or when they are congested by obstruction to the flow of blood through the liver or the heart; but no such mechanical arrangement can be fairly supposed to be the *chief* purpose of such a complicated organ in the economy. The spleen has been repeatedly removed, without any obviously injurious consequences; whence it appears, either that its function is not of vital importance, or (which is more likely) that it is discharged by some other organ in its stead. In some of the instances in which animals have been allowed to survive longest after removal of the Spleen, the *lymphatic glands* of the neighbourhood have been found greatly enlarged and clustered-together, so as nearly to equal the original spleen in volume; and hence it appears to be a fair inference, that the elaborating function of the spleen corresponds closely to that of the lymphatic glands.†

372. Having thus traced the steps by which the Blood is elaborated and

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* "Philosophical Transactions," 1846, p. 633.

† For a fuller discussion of the office of the 'Vascular Glands' than the limits of the present treatise allow, see the Author's "Principles of Human Physiology" (4th Ed.), §§ 481—491. Some novel and important anatomical details will be found in Dr. Franz Leydig's "Anatomisch-Histologische Untersuchungen über Fische und Reptilien," 1853.

prepared for circulation through the body, we have now to consider the fluid as a whole, and to study the nature of its chief constituents and the properties which they impart to it.—The Blood, whilst circulating in the living vessels, may be seen to consist of a transparent, nearly colourless fluid, termed *Liquor Sanguinis;* in which the *Red Corpuscles*, to which the Blood of Vertebrata owes its peculiar hue, as well as the *White* or *Colourless* corpuscles, are freely suspended and carried-along by the current.—On the other hand, when the blood has been drawn from the body, and is allowed to remain at rest, a spontaneous coagulation takes place, separating it into Clot and Serum. The clot is composed of a network of *Fibrin*, in the meshes of which the *Corpuscles*, both red and colourless, are involved; and the serum is nothing else than the liquor sanguinis deprived of its Fibrin. When the Serum is heated, it coagulates, showing the presence of *Albumen*. And if it be exposed to a high temperature, sufficient to decompose the animal matter, a considerable amount of earthy and alkaline *Salts* remains.—Thus we have four principal components in the Blood;—namely, Fibrin, Albumen, Corpuscles, and Saline matter. In the *circulating* Blood they are thus combined:*—

Fibrin Albumen Salts	In solution, forming Liquor Sanguinis.
Red Corpuscles,	—Suspended in Liquor Sanguinis.

But in *coagulated* blood they are thus combined:—

Fibrin Red Corpuscles,	Crassamentum or Clot.
Albumen Salts	Remaining in solution, forming Serum.

The solid matter of the blood also contains various *Fatty* substances which may be removed from it by ether. Some of these appear to correspond with the constituents of ordinary Fat; whilst another contains phosphorus, and seems allied to the peculiar fatty acids contained within the vesicles and tubes which form the nervous tissue (these phosphorised fats being found chiefly, if not exclusively, in the red corpuscles); and another has some of the properties of Cholesterine, the fatty matter of the Bile (§ 413).—Besides these, there are certain substances known under the name of *Extractive;* one group of which is soluble in water, and another in Alcohol. Of the precise nature of these, little is known. They have been aptly termed 'ill-defined' animal principles; and it is probable that they include various substances in a state of change, as well *progressive* (that is, intermediate between the crude material, and the tissue for whose nutrition they are being prepared), as *retrograde* (being products of the disintegration of the tissues, on their way to the excretory organs). To the former category probably belong the bodies which have been designated by Mulder as the binoxide and the tritoxide of protein; of which the first seems to be albuminous matter undergoing a change into the substance of hair, whilst the second appears to be similarly related to the gelatinous tissues. Under the latter, on the other hand, rank sugar, urea, uric and hippuric acids, creatine and creatinine, &c., which have been detected in it in very minute proportion in the state of health, but which accumulate in larger amount if their elimination be in any way checked.

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* The corpuscles of Frog's blood may be separated from the liquor sanguinis by filtration; but this experiment cannot be performed with Human blood, because its corpuscles are small enough to pass through the pores of any filter that allows the liquor sanguinis to permeate it.

373. The proportion of these components varies greatly in the different classes and orders of Animals. Thus in Man, in a state of health, we may reckon the whole solid matter of the blood at about 205 parts in 1000; the proportion of the several components averaging nearly as follows:*—

	Fibrin	2
	Corpuscles	150
Solids of Serum	Albumen	40
	Extractive Matters and Salts	11
	Fatty matters	2

In Carnivorous Mammalia, the average proportion of corpuscles is greater, whilst that of the solids of the serum is somewhat less, the fibrin remaining the same. On the other hand, in Herbivorous Mammalia, the proportion of corpuscles is considerably less, that of the solids of the serum is about the same, but that of the fibrin seems to be above the human average. In Birds, the total amount of solid matter is greater than in the average of Mammals; the excess being especially in the Red Corpuscles. In the cold-blooded Vertebrata, on the other hand, the proportion of solid matter, and especially of the Corpuscles, is greatly reduced; and the blood is manifestly paler and thinner.—In the blood of Man and the Mammalia in general, the Colourless Corpuscles usually bear a small proportion to the Red; and being nearly of the same aspect, they have until recently attracted but little notice. In Reptiles and Fishes, however, they differ so much in form, size, and general appearance, that they force themselves on the attention, even whilst the blood is moving through the capillaries; and they are the more easily watched, owing to the comparatively small number of Red corpuscles, to which they are found to bear an increasing proportion as we descend through the lower orders of the class of Fishes, until we come at last to the *Amphioxus*, in whose blood the red corpuscles are altogether wanting.—Of the relative amount of Fibrin in the blood of different animals, no other estimate has been formed, than that which rests upon the coagulating power of the liquid, which is much weaker in cold-blooded than in warm-blooded Vertebrata. —Of the variations in the proportions of other constituents, still less is known.

374. The new arrangement of the elements of the Blood, which takes place when it is withdrawn from the living body and left to itself, or even within the body when its vitality is lost, consists chiefly in the passage of its Fibrin from the state of solution to that of a fibrous network, in the meshes of which the Corpuscles are included. The rapidity of this change, and the completeness of its result, vary considerably; but are usually in an inverse ratio to each other. When the fibrin is imperfectly elaborated, so that the coagulum is deficient in firmness, the process

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* For the basis of this computation, which differs considerably from the usual statement in the small proportion of Albumen and the large proportion of Corpuscles, see the Author's "Human Physiology" (4th Ed.), § 154.

generally takes place rapidly, and is soon completed; but when it has undergone a higher degree of assimilation, so that it transforms itself into a definite fibrous tissue, the process is comparatively slow. The most perfect fibrillation is seen, not in blood itself, but in those effusions of modified liquor sanguinis, known as 'plastic' or 'organizable lymph,' which are thrown-out in the inflammatory process, or are effused in the first stage of the reparative operation consequent upon an injury. This may be due in part to the higher elaboration of the fibrin itself; and in part to the influence of vital force imparted from the living solids around (§ 343). If the influence of the living surface be continued, and vessels shoot from it into the primitive tissue so formed, this becomes part of the organised fabric; and thus we see that coagulation is not an indication of the *death* of the plastic fluid, but is a stage in its metamorphosis into a living solid. The tissue thus produced, however, is of a low order, and very prone to degenerate. When the blood has been withdrawn from the body, so that the coagulation takes place without any influence from a living surface, the fibrillated mass soon passes into decomposition; so that the process may then be considered as the last act of the life of the vital fluid. Even under the most favourable circumstances, it does not seem that the plastic force of the blood, or of the plasma effused from it, is able to develope any form of tissue higher than cells or simple fibres; for these are the sole kinds of organised structure, which ever directly result from the development of the 'nucleated blastema' thrown-out for the repair of injuries. And under less favourable circumstances, the same material resolves itself into a substance, *pus*, of far inferior character, in which no further organisation can ever take place, and which is only fit, therefore, to be cast out of the system.

375. The Albumen of the blood must be looked-upon as the *pabulum*, at the ultimate expense of which are formed all the azotized solids of the Animal body, as well as the fibrin, globulin, and hæmatin of the blood itself, and the albuminoid constituents of the secretions. It appears, however, to be entirely destitute of any *formative* capacity; for in no exudation which is purely serous, do we ever trace the slightest indication of spontaneous organisation; and its conversion into the various kinds of tissue, therefore, must be entirely due to *their* power of appropriating and transforming it. Still, the albumen of the blood is by no means identical with the raw material supplied by the digestive process; for, as already shown, an assimilating action is exerted upon it by the Liver (§ 366), and probably also by the 'Vascular Glands' generally, by which it is prepared for the organisation it is finally to undergo.—The *Fibrin* of the blood has been very commonly regarded (as formerly by the Author of this treatise) as that element which is immediately drawn-upon in the operations of nutrition; being the intermediate stage between the crude albumen and the solid tissues. This opinion rested in part upon the current doctrine, that fibrin is the constituent of muscle; and in part upon the assumption, that as fibrin is more endowed with vital properties than any other of the liquid components of the blood, so as to be capable of passing by itself into the condition of an organised tissue, it must be the one most readily appropriated by the various parts of the solid fabric, as the material of their growth and development. It is now certain, however, that, so far from there being any correspondence between blood-

fibrin and muscular substance, there is a very decided difference between them, muscle-substance in fact, being more like albumen;[*] whilst as the fibrous reticulation formed by the coagulation of fibrin bears more resemblance to the white fibrous tissue, than to any other tissue in the body, it would seem as if its special endowments had reference more to the formation of this simple connective material, than to the nutrition of tissues of higher endowments. And this view is confirmed by the fact, that the points in which fibrin differs chemically from albumen, are such as indicate some relationship to gelatin. We seem justified in regarding fibrin, therefore, as the special pabulum of those *connective* tissues, whose vital endowments are so low; and as serving, by the peculiar formative power which it derives from the special elaboration it has received, for the independent generation of those tissues, wherever and whenever there may be a demand for them. Independently of any such office in the general economy, however, the importance of fibrin as a constituent of the blood cannot be over-estimated: for on the viscidity which it imparts, the retention of the blood within the walls of the vessels, and even its unobstructed movement through them, appear (from the experiments of Magendie) to be due; and it is entirely on the coagulating power of the blood, that the cessation of hemorrhage from even the most trifling injuries, is dependent; whilst the adhesion of incised wounds, still more the filling-up of breaches of substance, require as their first condition, that either the blood, or matter exuded from it, should be able to assume the form of fibrous tissue.[†]

376. The offices of the *Red Corpuscles* of the blood are still involved in considerable obscurity. They are, in fact, floating cells filled with a mixture of substances, the composition of which differs considerably from that of the liquor sanguinis which surrounds them. For the principal organic constituent of this mixture is the substance termed *Globulin*, which is allied to albumen in the proportions of its ultimate elements, but which differs from it in certain of its reactions; and with this is associated the peculiar colouring substance *Hæmatin*, which departs widely in composition both from albumen and gelatin, and contains 7 per cent. of iron; the proportions of these two compounds, in the fluid of the red corpuscles, being about 17 of the former to 1 of the latter. The phosphorised fats of the blood, again, are contained within the red corpuscles; and these also include nearly the whole of the potash-salts which the blood may possess, the alkalinity of the liquor sanguinis being due to soda.[‡] Now, as the former of these last-named peculiarities indicates a relationship between the Red corpuscles and the Nervous system, which is further rendered probable by the presence of a pigmentary matter much resembling

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[*] See Liebig, in "Ann. der Chem. und Pharm.," Bd. lxxii.

[†] A reaction has recently taken place against the once-prevalent doctrine that Fibrin is the immediate *pabulum* of the solid tissues generally; the hypothesis having been put-forth by Zimmerman, and espoused by Mr. Simon and some other Pathologists in this country, that Fibrin is one of the elements of the circulating fluid, which is in a state of retrograde metamorphosis, and is therefore on its way to be eliminated by the excretory organs. The Author's objections to this doctrine, and a fuller view of the relations of Fibrin to the animal economy, will be found in his "Human Physiology" (4th Ed.), §§ 192, 193.

[‡] See Dr. G. O. Rees in "Philosophical Magazine," Vol. xxiii., p. 28; and Lehmann's "Lehrbuch der Physiologischen Chemie" (2nd Ed)., Band II., p. 131.

hæmatin in the grey vesicles of the nervous centres;—and as the latter indicates a like special relationship with the Muscular substance, which (as Liebig has shown) is as remarkable as the red corpuscles for the almost exclusive presence of *potash*-salts, whilst the liquor sanguinis is charged with *soda;*—we may perhaps surmise without much improbability, that it is one special object of the red corpuscles to prepare or elaborate materials, which are to become subservient to the nutrition of these tissues. Moreover, as the corpuscles seem to possess more power of absorbing oxygen and carbonic acid, than do any other constituents of the blood, we may look upon them as specially (but not exclusively) carriers of those gases between the respiratory organs and the tissues (§ 207); and in so doing, they will be peculiarly subservient to the vital activity of the Nervo-muscular apparatus, since it is one of the special conditions of its energetic operation, that oxygen shall be conveyed to it by the arterial current, and that carbonic acid, which is one of the products of its disintegration, shall be conveyed away. And this view is in complete harmony with the fact, that the proportion of Red Corpuscles in the blood bears a close relation to the amount of Respiratory power in different classes of Vertebrata; being greatest in Birds, nearly as great in Mammals, very low in most Reptiles, and varying considerably among Fishes.—Still greater difficulty exists in determining the functions of the White or *Colourless Corpuscles,* which have not been obtained for analysis in a separate state, and of whose composition, therefore, nothing certain is known. Their close correspondence with the colourless corpuscles of the blood of Invertebrata, and the appearances occasionally presented by them, indicative of a progressive transformation into *red* corpuscles, justify the inference that they are to be considered as holding an intermediate place between the nuclear corpuscles of the Chyle and Lymph (together with those of the 'Vascular Glands,' which also probably find their way into the blood-current), and the completely-developed coloured cells. Yet there are indications that during this transition-stage of their development, they exert an influence in the production of the fibrinous constituents of the blood; and it does not seem impossible that under the general designation 'colourless corpuscle,' more than one kind of cell may be ranked.*

377. The *Fatty* matters of the blood are obviously destined to furnish the contents of the adipose and nervous vesicles; whilst their presence seems also to be required in the early stages of the production of cells generally. One of the principal sources of their expenditure, however, is that combustive process by which the heat of the body is maintained (§ 116); and the amount deposited in the tissues as fat, may be looked-upon as the surplus of the quantity ingested, over and above that which is thus consumed. The quantity of fatty matter in the blood is liable to sudden augmentation, from the introduction of a large quantity furnished at once by the alimentary materials, so that the serum presents the milky aspect of chyle; and this excess will continue, until the surplus has been eliminated, either by the combustive, the nutritive, or the excretory operations.—Of the uses of the various *Inorganic Compounds,* which, as being uniformly present in the Blood, must be considered among its

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* For a discussion of this question, see the Author's "Human Physiology" (4th Ed.), §§ 195, 196.

integral constituents, the following may be considered to be those best determined. The presence of the phosphate and carbonate of Soda seems to have reference chiefly to the maintenance of the alkalinity of the blood, on which its power of holding albuminous matters in solution essentially depends, but has also the very important office of increasing the absorptive power of the serum for gases; whilst chloride of sodium is needed alike for the conservation of the organic components of the blood in their normal condition, and for the supply of the salt which enters into the composition, not only of the solid tissues, but also of all the secreted fluids, as also to furnish the hydrochloric acid of the gastric fluid (§ 163) and the soda of the bile (§ 413). The salts of Potash, on the other hand, appear to be specially required for the nutrition of the muscular substance; while the Earthy salts are required for the consolidation of the harder tissues, into which some of them enter very largely. Iron, like the alkaline salts, appears to have some essential purpose in the blood itself, since it enters into the composition of the red corpuscles in larger proportion than it does into any of the solid tissues; and its presence in sufficient amount is an essential condition of their production.

378. Although the proportions of the different components of the Blood of Man, or any other of the higher animals, are continually undergoing change by the introduction of new materials, and by the perpetual withdrawal of those which have become prepared for the production of tissues, yet all such changes have their limits; and taken as a whole, the composition of this fluid, in each species, exhibits such a remarkable constancy (within the limits of health), that we can scarcely fail to recognize in it some such capacity for self-development and maintenance, as that of which we admit the existence in the solid tissues. And this idea will be found less strange, when it is borne in mind that the first blood is formed by the liquefaction of the primordial cells of the embryo; and that, notwithstanding the continual change in its components, it still retains its identity through life, in no less a degree than a limb or an eye; the material changes in which, though less rapid, are not less complete. Looking again, to the undoubted vitality of the Corpuscles, and to the strong ground for regarding the Fibrin also as possessing vital endowments, we cannot but perceive that the Life of the Blood is as legitimate a phrase, and ought to carry as much meaning in it, as the Life of a Muscle.

379. We shall now enquire how far any approximation can be found among the lower tribes of Animals, to that process of Assimilation, whose principal steps have thus been traced in the beings of highest organization. We may observe, however, in the first instance, that there are two reasons why the first approaches to such an operation might be expected to be very slightly marked. For, in the first place, in proportion to the homogeneousness of the fabric of the body, and to the absence of specialization in its functions, might we anticipate that the composition of the nutritive fluid would be simple, and its vital endowments low. And, secondly, in proportion as the several parts live *for* and *by* themselves, should we expect to find a want of specialization in the apparatus of assimilation; the nutritive fluid being rather elaborated by its contact with the living solids of the body generally, than by its passage through any one

organ or set of organs, or by the agency of its own floating corpuscles. As Dr. T. Williams has justly remarked,* the solids of the lower Invertebrata are more completely saturated with their fluids, than they are in higher animals; and there is, therefore, the greater probability that the fluids undergo a preparatory change, either in the interior-of, or between, their cells, to qualify them for the work of histogenesis.—In all *Polypifera*, it will be remembered that the general cavity of the body communicates freely with the gastric cavity; so that the fluid which passes into it for the purposes of nutrition, must be regarded as the immediate product of digestion, or as *chyme*. This fluid contains scattered corpuscles, by the movement of which its own motions are recognized; and these corpuscles are minute spherical particles, apparently albuminous, mingled with oil-particles. Some few appear to be nucleated, whilst others are charged with minute granules; and in *Actinia*, according to Dr. T. Williams, they are occasionally seen to contain secondary cells. The fluid that has remained for a time in the splanchnic cavity, is found to contain a small quantity of Albumen; but it undergoes no spontaneous coagulation.—In *Acalephæ*, too, the only nutritive fluid is the chymous product of digestion, which moves in the gastro-vascular system. Its corpuscles are larger than those of Zoophytes, and are more laden with granular and adipose contents: their cell-membrane, too, is more distinct; and they sometimes present a blueish tint. The fluid in which they float has a 'molecular base;' but it gives no indication of the presence of fibrin.—A higher type, however, is attained in Echinodermata. The splanchnic cavity being here shut-off completely from the alimentary canal, the fluid which it contains must be likened, not to chyme, but to *chyle*; but its characters do not show any decided advance upon those of the preceding. Its corpuscles, indeed, are described by Dr. T. Williams as looking like spherules composed of hard and very minute granules of coagulated albumen, without any detectible nucleus or cell-wall, destitute of oily particles, and readily diffused into their individual molecules; in all these particulars being *less* advanced (if his description be correct) than the vesicular corpuscles of the classes already named. The fluid is rendered cloudy by heat and nitric acid; but though albumen is thus indicated, there is no trace of fibrin. The fluid of the (so-called) sanguiferous system (§ 215) differs from that of the splanchnic cavity in no other respect, than in containing a larger proportion of solid constituents; and it seems not improbable that the purpose of this system is only to concentrate (so to speak) the nutritive force of the chylaqueous fluid upon some of the more important viscera, and not, as in higher animals, to distribute a fluid of more special endowments. In the *Sipunculida*, which form a link between this class and the Annelida, the corpuscles are flat and irregularly-oblong; each has a bright, small, highly-refractive nucleus; and the colour is dissolved in the fluid between the nucleus and the cell-wall—thus remarkably foreshadowing the regular blood-corpuscle of higher animals.

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* "Brit. and For. Med. Chir. Review.," Vol. XII., p. 484.—The details in the text, on the subject of the nutritive fluids of the Invertebrata, have been derived in part from Dr. T. Williams's Papers in that Journal, and from his Memoir 'On the Blood-proper and Chylaqueous Fluid,' in "Philos. Transact.," 1852; and partly from Mr. Wharton Jones's Memoirs 'On the Blood-Corpuscle considered in its different phases of development in the Animal series,' in "Philos. Transact.," 1846.—In the *interpretation* of these facts, however, (especially in regard to what is to be considered as *blood* in the Annelida), the Author has followed his own judgment.

380. Passing on, now, to the lowest members of the *Articulated* series, we first come to those *Cestoid Entozoa,* among which no distinct nutritive fluid can be said to exist; their aliment being provided, not by a process of gastric digestion, but by direct imbibition through their entire surface. And in the *Trematoda,* whose digestive sac is so closely embraced by the surrounding tissues that there is no proper gastric cavity, we return to the Zoophytic type, in which the immediate product of digestion is applied to the purposes of nutrition. This chymous fluid of the gastric cæca accordingly presents a richly-corpusculated aspect; its corpuscles not being formless molecules, but consisting of a cell-wall and granular contents, frequently with a definite nucleus; and exhibiting constant differences in different species. Where any fluid can be distinguished in the perigastric areolæ, it is non-corpusculated; as is also the fluid of the 'aquiferous' system of vessels, alike in the Entozoa and Turbellaria, notwithstanding that is frequently coloured.* In the *Nematoid* Entozoa, a distinct perigastric cavity exists; and the fluid which it contains, though rich in albumen, is destitute of corpuscles. The absence of these may not be improbably due to the circumstance that the nutritive fluid has already undergone the requisite elaboration in the body of the animal from which it is drawn by these parasites; just as the vegetable parasites which derive their supply from the elaborated sap of the plants they infest, have no leaves wherewith to exercise any converting power upon it for themselves (§ 356).—The curious question which next presents itself, in regard to the circulating fluids of the *Annelida,* has already been more than once alluded-to (§§ 219, 292). The fluid of the splanchnic cavity here presents a character very nearly corresponding with that of the fully-elaborated chyle of Vertebrata, save that it is not so opalescent. Its usual characters may be peculiarly well seen in the cirrhi of the *Terebella;* where it is observed to be a somewhat milky liquid, containing large oval flattened vesicles, filled with oil-molecules and granules, with other fusiform corpuscles, destitute of granular contents and pellucid. It is stated by Dr. T. Williams, that the larger corpuscles not unfrequently burst in the field of the microscope, and that their semi-fluid contents coagulate as they flow out. The fluid itself is albuminous. The size, form, and general characters of the corpuscles differ in different species of this group; and two instances are recorded by Dr. T. Williams, in which the corpuscles have a decided red tint.† On the

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* See Dr. T. Williams, in "Ann. of Nat. Hist.," 2nd Ser., Vol. XII., p. 333, et seq. —The aquiferous system of vessels in these tribes is designated by Dr. T. Williams as undoubtedly 'chylaqueous;' on what principle, however, the Author must confess himself to be at a loss even to guess. The existence of the 'water-vascular system' is altogether ignored by Dr. Williams; the general correctness of whose interpretations may be in some degree estimated by the fact, that he asserts "the large branched, flocculent organ, forming the bulk of each segment in *Tænia* and *Bothriocephalus,*" which all other zoologists and anatomists without exception regard as an ovary, to be "really the alimentary organ, opening externally by an orifice proper to each segment!"

† These are the genera *Glycera* and *Clymene,* the former of which has been stated by M. De Quatrefages to have coloured globules in its *blood,* the liquid itself being colourless. The Author cannot but think it probable that this generally-accurate observer has been misled in his interpretation by the unusual nature of the phenomenon; and believes it to be much more likely that the 'chylaqueous fluid' of an Annelid should have coloured corpuscles, than that its 'blood' should have corpuscles floating in a colourless fluid.

other hand, the fluid which is commonly designated as the 'blood' of the Annelida is destitute of any morphotic elements whatever, and cannot be observed either to fibrillate or to coagulate by heat. It possesses, therefore, none of the attributes of true *blood*, save its colour; and can scarcely be supposed to take any considerable share in the *nutrition* of the body, for which it is obvious that provision is made in that diffusion of the chylaqueous fluid, which is so elaborate in many instances as to constitute a real circulation. Its colour, in fact, which is sometimes pale-yellow or orange, sometimos of a full red or green, is its chief distinguishing attribute; yet as approximations to these hues are exhibited by the contents of the water-vascular system in many of the lower Articulata, no adequate reason is hence derivable, for assigning to it a character which the position of this group in the series would render it highly improbable that it should possess. As already pointed-out (§ 308), the fluid of the water-vascular system has probably an express relation to the *respiratory* function; and it is where no special provision exists for *its* aeration, that we find the so-called 'blood-vascular' system attaining its highest development. If the view already given of its homologies should prove correct, it is obvious that it is the chylaqueous fluid of the Annelida, and not their blood, which is homologous with the blood of Insects and Crustacea; for although their nutritious fluid circulates through a more definite system of vessels and of circumscribed lacunæ, that system still communicates freely with the visceral cavity, the contents of which are of the same nature with theirs. On the other hand, the so-called blood-vascular system of the Annelida attains a development to which nothing is comparable among the higher Articulata, save that of the tracheal apparatus, with which it may be considered homologous. It is remarked by Dr. T. Williams, that for some time after the emergence of the young from the ovum, and before the development of the branchial, pedal, and tentacular appendages, the chylaqueous fluid contains no corpuscles; as the worm advances in growth and development, the corpuscles slowly appear; the (so-called) blood and blood-vessels being produced, however, before they are distinguishable.

381. The higher Articulata are characterized by one general type of nutritive fluid; that, namely, which in the early embryonic condition of most among them is obviously 'chylaqueous,' being colourless and richly-corpusculated, and moving freely in the splanchnic cavity; but which gradually becomes more limited and enclosed, and sometimes undergoes a considerable change in its own character. In the adult *Myriapoda*, the corpuscles are very numerous, and are described by Dr. T. Williams as presenting three principal varieties:—1, a large pellucid nucleus surrounded by a few granules; 2, an orbicular body in which the granules are so augmented in number as almost to conceal the nucleus; 3, an ovoid or oat-shaped corpuscle, in which the nucleus has reappeared. In none of these can the existence of a proper cell-wall be demonstrated; but their particles seem to be held-together by some tenacious self-coagulating substance; for, when the corpuscles burst in the field of the microscope, a fibrillation is seen to take place in the matter that is set free. The classes of Insects, Crustacea, and Arachnida present in their perfected states a more advanced form of the same corpuscle; the type of which is a flattened oval cell, having a distinct cell-wall, and a conspicuous nucleus,

surrounded by minute granules, the contents of this cell fibrillating when liberated by its bursting. It has been observed by Mr. Newport,* that the 'oat-shaped' corpuscles are most numerous in the larva at the period immediately preceding each change of skin; at which time the blood is extremely coagulable, and evidently possesses the greatest formative power. The smallest number are met-with soon after the change of skin, when the nutrient matter of the blood has been exhausted in the production of the new epidermic tissue. In the Pupa state, the greatest number are found at about the 3rd or 4th day subsequent to the change; when preparations appear to be most actively going-on, for the development of the new parts that are to appear in the perfect Insect. After this, there is a gradual diminution, the plastic element being progressively withdrawn by the formative processes; until, in the perfect Insect, very few corpuscles remain. When the wings are being expanded, however, and are still soft, a few oat-shaped corpuscles circulate through their vessels; but as the wings become consolidated, these corpuscles appear to be arrested, and to break-down in the circulating passages; supplying, as Mr. Newport thinks, the nutrient material for the completion of these structures, which subsequently undergo no change. The blood of Insects also contains cells that are more distinctly nucleated; the proportion of which seems to increase in the Imago state, whilst that of the more granular oat-shaped corpuscles diminishes. The blood of the Crab is described by Mr. Wharton Jones as possessing a pale reddish-gray or neutral tint, and as separating spontaneously into a spongy-looking mass and a serous fluid; the former chiefly consists of aggregated corpuscles, there being apparently but little fibrillating material; the latter contains enough albumen to cause it to coagulate by heat. The corpuscles are stated by Prof. Graham to contain a sensible quantity of iron, perhaps as much as red corpuscles.† Is is obvious, therefore, that in these more elevated forms of the Articulated series, the circulating fluid presents a close approximation to the blood of Vertebrated animals; its nearest representative among them, perhaps, being the chyle of the thoracic duct.

382. In ascending through the *Molluscous* series, in like manner, we find a like gradation in the character of the circulating fluid, from the thin and almost watery contents of the visceral sac in the Bryozoa, with a few minute irregular corpuscles floating in it here and there, to the richly-corpusculated and spontaneously-coagulable blood of the Cephalopods, which is still, however, a 'chylaqueous fluid,' in so far as it passes through the splanchnic cavity in the course of its circulation. In this, as in the preceding series, a gradation in the character of the morphotic elements is traced by Mr. Wharton Jones (loc. cit.) from (1) the 'coarse granule-cell' (2) to the 'fine granule-cell,' and thence to (3) the 'colourless nucleated cell', which is the highest form of corpuscle in the blood of Invertebrata. All these stages have their antitypes in the chyle, lymph, and blood of vertebrated animals; and the last-named form undergoes a further development in Oviparous Vertebrata, into (4) the 'coloured nucleated cell', which is the characteristic type of *their* blood-discs. The 'non-nucleated coloured cell', which constitutes the red blood-disc of Mammals,

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* "Philosophical Magazine," May, 1845.

† "Philosophical Transactions," 1846, pp. 89, 105.

is regarded by Mr. Wharton Jones as the escaped nucleus of the preceding, which has itself taken the form of a cell; but other observers agree in considering it a more advanced stage in the development of the nucleated blood-cell of the Oviparous Vertebrata, from which the nucleus has disappeared.

383. In the foregoing account of the formation, composition, and properties of the Blood, it has been shown that the Albuminous materials obtained from the aliment, or received back from the body itself, are gradually prepared for organisation, whilst yet remaining in the fluid state; and that when they have attained the condition of Fibrin, they have been so far modified by the vitalising influences to which they are subjected, that they are capable of spontaneously passing into a state of incipient organisation. The production of all the higher forms of organised tissue, however, is manifestly dependent, not upon the plastic properties of the blood alone, but upon the Formative powers of the tissues themselves; each tissue, from the time when it first presents its characteristic structure in the embryo, continuing to grow, develope, and maintain itself, at the expense of the materials which it draws from the blood. It would be inconsistent with the character of this treatise to enter into details upon this subject, which will be fully considered in the GENERAL PHYSIOLOGY; all that is here appropriate being a brief account of the mode in which the *elementary* forms of Animal tissue, namely *cells* and *fibres*, are produced.

384. The history of the Animal Cell, in its simplest form, is essentially that of a Vegetable cell of the lowest kind. Every cell lives *for* itself, and *by* itself, like each of the solitary cells of the humblest Protophytes; and if the necessary conditions be furnished (these being essentially a due supply of nutriment, and a proper temperature), it may continue to live and to grow, and may go through all the phases of its development, quite independently of the organism of which it originally formed part. Of this we have numerous examples in the artificial implantation of parts of one body upon or within another; the graft uniting itself with its new stock, and continuing to grow after its own fashion at the expense of the nourishment thence derived. But a still more remarkable example is normally and constantly presented by the spermatic cells of certain animals, such as the Decapod Crustacea * and certain Nematoid Entozoa ;† which are cast-forth from the organs of the male in which they were generated, and are transferred into the body of the female, when as yet they are in a comparatively early stage of their own development; the spermatozoa being not then formed within them, but being produced during the subsequent life of the cells, which apparently goes-on as favourably within the generative passages of the female, as it would have done within the organs in which the spermatic cells were at first formed, the requisite conditions being duly supplied. All the component cells of any one organism may be considered as the descendants of the primordial cell in which it originated; but the methods of their production are by no means identical in every instance, an end essentially the same being brought about by means which appear (at least) to be very different. The various modes of cell-development may however be reduced to two prin-

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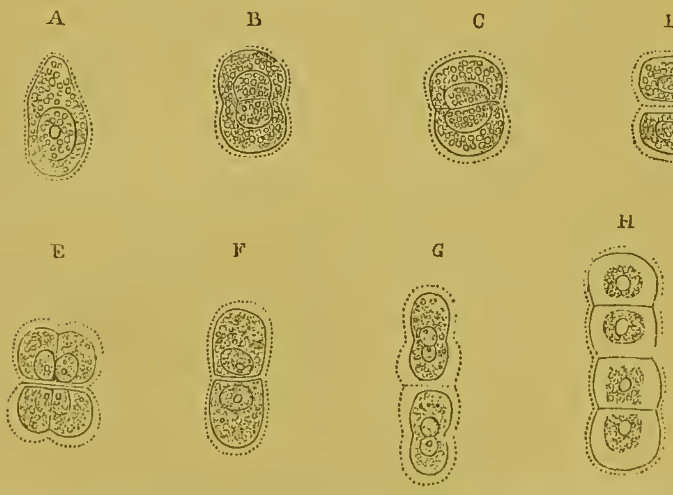
* Mr. H. D. S. Goodsir, in "Anatomical and Pathological Observations," p. 39.

† Dr. Nelson, "Philosophical Transactions," 1852, p. 565.

cipal forms;—that, namely, in which the new cells arise *from* or *within* pre-existing cells, being produced by the subdivision either of the cells themselves, or of their nuclei, which is termed *endogenous* development; —and that in which they originate in germs developed *de novo* in the midst of an organizable 'blastema,' which has been prepared by a previous exercise of vital force, and which still requires the continued operation of that force *ab extra* for its due organization (§ 339). Each of these modes of *cytogenesis*, or cell-development, will now be separately considered.

385. The multiplication of Cells by *duplicative subdivision*, which we have seen to be the most common form of cytogenesis in the Vegetable kingdom, is observed to take place also within the Animal body, after a manner essentially the same, in most cases in which new parts are being developed in continuity with the old. The most characteristic example of it is seen in the early Embryo (§ 73); which, at first consisting of but a single cell, has its number of cells augmented by such duplication, to 2, 4, 8, 16, 32, 64, &c. The same process may also be watched through the whole of life in Cartilage; and it is one of the means by which the Red Corpuscles of the blood are multiplied in an early stage of their development. Where a distinct 'nucleus' exists, however,—as is the case in most Animal cells—the process of subdivision seems frequently to commence in *it;* for before any distinct inflection of the cell-wall can be perceived, the nucleus may be seen to elongate, and to show a tendency to subdivision into two equal parts. Each of these, when completely separated, draws round it a portion of the contents of the cell; so that the cell-wall, which at first exhibits merely a sort of hour-glass contraction, is at last inflected so far as to constitute a complete partition between the two halves of the original cell; and these henceforth become two independent cells, which may go through the same process in their turn (Fig. 165, A—D).

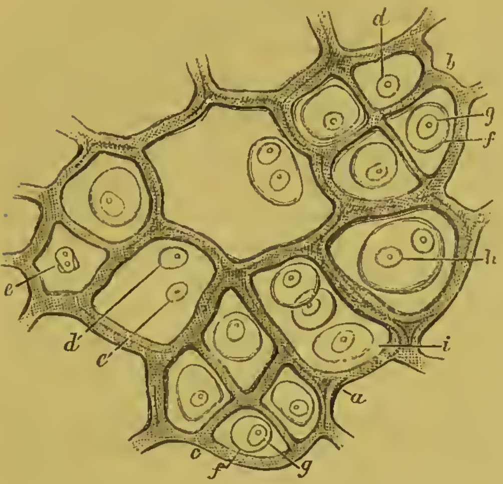
FIG. 165.



Multiplication of *Cartilage-cells* by subdivision:—A, original cell; B, the same, beginning to divide; C, the same showing complete division of the nucleus; D, the same with the halves of the nucleus separated, and the cavity of the cell subdivided; E, continuation of the same process, with cleavage in *contrary* direction, to form a cluster of four cells; F, G, H, production of a longitudinal series of cells, by continuation of cleavage in the *same* direction.

The repetition of this operation may take-place either in the same or in the contrary direction, so as to produce four cells, either linearly arranged (E, F, G), or clustered together (H); and this duplication may go-on upon the same plan, until a large mass has been produced by the subdivision of a single original cell. In ordinary Cartilage,* it is most common to see the cells forming clusters; but in Cartilage which is being prepared for ossification, we see long lines of cells, which have been obviously produced by the first of these methods of multiplication.

Fig. 166.



Section of branchial Cartilage of Tadpole of *Rana paradoxa*:—*a*, *b*, *c*, intercellular substance, with which the walls of the parent-cells are incorporated; *d*, single nucleus; *e*, nucleus dividing into two; *d'*, *e'*, two nuclei in one cell, formed by division of single nucleus; *f*, secondary cell, forming around nucleus *g*; *h*, two nuclei within single secondary cell; *i*, three secondary cells, within one primary cell.

386. Not unfrequently, however, the multiplication of cells takes place, not so much by the subdivision of the pre-existing cell, as by the development of new cells in its interior; these appear to take their origin in the nucleus, which subdivides into two or more portions, each of them drawing a portion of the contents of the primary cell towards itself, and becoming converted into a cell by the development of a cell-wall around this; and they gradually increase in dimensions, until they come to occupy the entire cavity of the primary cell, and may so distend its wall by their further enlargement, that it can no longer be distinguished. Of this method of cell-formation, also, we have examples in cartilage, especially in its early stage of development, when its growth is rapid (Fig. 166); but we there seldom see more than three or four cells thus generated within a primary cell at any one time. It is in structures of more rapid growth, such as granulations,† and especially in cells of a cancerous or malignant character, whose speedy development and no less speedy degeneration are among their most distinguishing features, that we most frequently witness the subdivision of the nucleus into a considerable number of parts, and the development of numerous cells at one time within the cavity of

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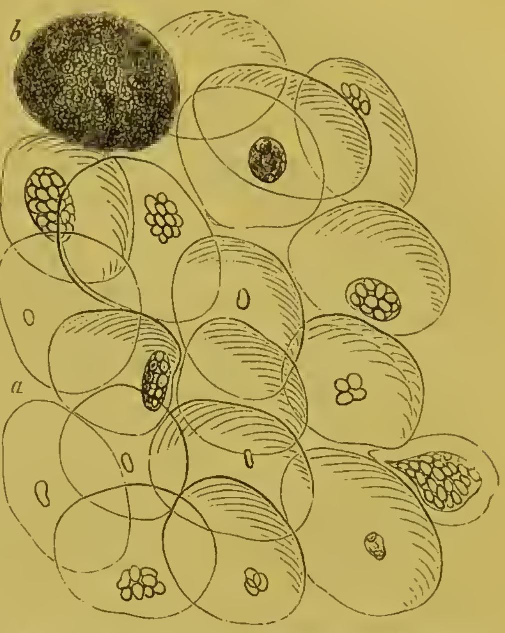
* It is thought by Dr. Leidy, who has carefully studied this process in Cartilage (see his valuable paper 'On the Intimate Structure and History of Articular Cartilages,' in the "Amer. Journ. of Med. Sci.," April, 1849), that the direction of the subdivision is determined by that in which there is least resistance to the extension of the group of cells; but such can scarcely be the case in regard to the embryonic mass, the cells of which, if this were the sole determining influence, would continue to multiply on a uniform plan; instead of which, as soon as they have arrived at a certain degree of minuteness of subdivision, a diversity of arrangement begins to show itself in the component parts of what was previously a homogeneous assemblage.

† It is stated by Mr. Paget ("Lectures on Surgical Pathology," Vol. I., p. 185), that in granulations, especially such as are formed on bones, there are often to be found large compound cells of oval form, and as much as 1-250th of an inch in diameter, containing eight, ten, or more nuclei, which have been derived by subdivision from the nucleus of the primary cell, and which are probably destined to be the nuclei of as many separate cells.

each primary cell (Fig. 167). The same method may often be recognized, however, in the development of cells within Glandular follicles; for where each follicle is a single primary cell, and its nucleus remains persistent as a 'germinal centre,' subsequently to its becoming a follicle by the rupture or thinning-away of a part of its cell-wall, it appears to be by the continual sprouting of new cells from this nucleus, that the materials of the secretion are eliminated from the blood (Fig. 175).—As a general rule, however, it may be remarked, that the production of a large number of cells within a single primary cell only takes place when this new brood is *not* to form a permanent part of the organism, or to be itself the originator of a subsequent growth. It would seem, indeed, as if this rapid method of multiplication occasioned an exhaustion of vital force; so that the cells thus generated are incapacitated for any other purpose; whilst the comparatively slow method of duplicative subdivision may be repeated time after time, to an extent to which it is impossible to assign a limit, each pair of cells thus produced having an equal capacity with its progenitors for going through that process.

Fig. 167.



Endogenous cell-growth, in cells of a Meliceritous Tumour:—*a*, cells presenting nuclei in various stages of development into a new brood; *b*, primary cell, completely filled with a new brood of young cells, which have originated from the granules of its nucleus.

387. There are cases, however, in which cells are developed, without any direct connection with pre-existing cells, in the midst of a *blastema* or formative fluid poured-out from the blood. Still it is uncertain to what extent this is to be considered as one of the ordinary modes in which the elements of the tissues are produced and increased; for it has been hitherto chiefly observed in cases in which a plastic exudation has been poured-out for reparative purposes, or in which a structure of an abnormal character is being generated. The first step in the process usually appears to be the aggregation of some of the minute molecules which the fluid or semi-solid blastema contains, so that they form little rounded masses, or nuclei, from which the new cells originate. The mode in which the cell-wall is formed, does not appear to be by any means constant. Sometimes it seems to rise and separate itself from the nucleus itself, as if it were formed by the melting-together of molecules precipitated-upon or attracted-to the nucleus; but more frequently it appears to be generated by the expansion of the wall of the nucleus itself; in either case, however, commencing to enlarge and separate itself from the nucleus, by the endosmosis or assimilation of fluid from the surrounding blastema.* But there are other cases in which the nuclear particles

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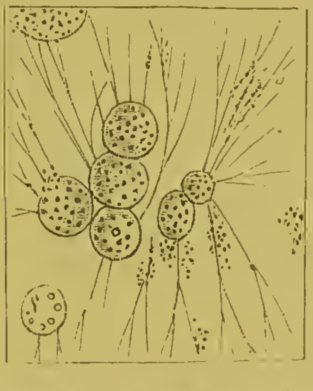
* See Prof. Bennett's Treatise "On Cancerous and Cancroid Growths," p. 146.

appear to draw around them certain components of the substance in which they lie, before any cell-wall can be discerned, this being subsequently generated around this collection, which then constitutes the contents of the newly-formed cell. This first-formed nucleus may be persistent, and may take a part in the subsequent vital actions of the cell, of whatever kind these may be; or it may be superseded by a second nucleus, which subsequently makes its appearance in some other part of the cell-wall.—It seems probable that the first formation of the chyle- and lymph-corpuscles, which subsequently develope themselves into blood-corpuscles, takes place from free nuclei; and it has been maintained by some that, the epidermis and epithelium are likewise formed in the same manner;—both these views, however, require confirmation.

388. That *all* the Animal tissues have their origin in Cells, so that even the widest diversities of type are reducible to the same category, was the doctrine originally put forth by Schwann, who first attempted to generalize the phenomena (most of them discovered by his own observations) which are presented by their development. By subsequent research, however, it has been shown that this statement was too hasty; and that, although many of the tissues retain their primitive cellular type through life, and many more are evidently generated from cells which subsequently undergo metamorphosis, there are some in which scarcely any other cell-agency can be traced, than that concerned in the preparation of the plastic material. This would seem to be the case especially with those *Simple Fibrous Tissues*, which make-up a very considerable proportion of the bulk of the body. For although it seems indubitable that they *may* be formed by the transformation of cells,* and although they probably *are* thus generated in the first development of the organism, yet their subsequent production (especially in the reparation of injuries under favourable circumstances) seems to be effected by the fibrillation of an 'organizable blastema.' Even here the course and direction of the fibres seem often to be determined by the nuclear particles which the fibrillating substance includes; for in the reproduction of tendinous tissue, as observed by Mr. Paget,† the nuclei are formed and become elongated *before* any fibrillation is visible, and the fibrillation takes place in the direction in which they lie, so that each nucleus is imbedded in a fasciculus of fibres; and a similar relation has been pointed-out by Mr. Addison,‡ who has remarked that the fibres which are formed during the coagulation of the liquor sanguinis or in other plastic exudations, often seem to radiate from the cells or nuclear corpuscles which these fluids may contain (Fig. 168). These facts give a sufficient explanation of the presence of nuclei in the

FIG. 168.



Cells with Radiating Fibres, from the fluid of the vesicles of Herpes labialis.

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* "Lectures on Surgical Pathology," Vol. I., p. 182.

† Op. Cit., p. 187.

‡ "Second Series of Experimental Researches on the Process of Nutrition in the Living Structure," p. 5; and "Third Series," p. 7.

midst of the simple fibrous tissues, which has been adduced in support of the doctrine of their origin in cells.—A very marked example of the production of fibres in the midst of an organisable substance, without any direct intervention of cells, is afforded by *Fibro-Cartilage;* the various forms of which present every gradation, between the perfectly homogeneous intercellular substance of ordinary Cartilage, and a distinct Fibrous tissue. Here, too, it is possible that, although the fibres do not themselves originate in the transformation of cells, the cells of the cartilage may exert such a determining agency in their production, as appears to proceed from the nuclei in the cases previously referred-to.—Of all the varieties of Fibrous tissue thus generated, it may be stated that their function is simply mechanical; that consequently the performance of that function does not depend upon a continuance of vital activity; and that they do not seem to possess that power of *self-formation* which is characteristic of the cellular tissues, but for the most part depend, for their production, maintenance, and regeneration after injury, upon the formative power of the Blood (§ 374).

389. The leading conclusions in regard to the Chemistry of the Animal Body, to which the Chemico-physiological labours of recent times appear to point, may be summed-up as follows:—

I. The Organic materials indispensable for the *genesis* of tissue, consist of *Albuminous* and *Fatty* compounds.—The former present themselves under various aspects, in the Vegetable as well as in the Animal kingdom, all being reducible, however, to the ordinary state of Albumen by the digestive process; and in their natural state of combination, they include most of the inorganic substances which are required in addition. There is no reason whatever to believe, that Albuminous compounds can be generated within the animal body, by the transformation of substances belonging to an entirely different type.—The latter are directly afforded by ordinary animal food, and by many kinds of vegetable productions; and it seems to be when they are thus supplied, that they are most readily made available in histogenesis. They may be produced within the body, however, by the metamorphosis of either Albuminous or Saccharine compounds.

II. The great mass of those tissues of the body which belong to the *cellular* type, is generated at the expense of Albuminous matter (fat-particles, however, being intimately blended with this in an early stage of cell-formation); of this we have a notable example in the case of Muscular tissue; but the cell-walls of all other textures would probably be found, if they could be entirely freed from their contents, to have the same composition. The molecular condition of the particles composing the amorphous coagulum and the living cell, however, must be entirely different, even if they be altogether *chemically* identical; and the latter exhibits distinctive *vital* properties, in virtue of the organizing process to which its material has been subjected. Not merely the cell-walls, but the cell-contents of these tissues (with the exception of those concerned in the act of excretion), seem to be derived from the Albuminous or from the Fatty constituents of the blood: this seems clear, for example, in regard to the globulin and hæmatin of the red corpuscles of the blood, and the horny matter of the epidermis and its appendages, which must have their source in the former; and also with respect to the contents of the adipose and nervous vesicles, which must be drawn wholly or in part from the latter. Whether, in the construction of the tissues of this class, the Albumen of the blood may serve directly as the *pabulum* for the production of cells, or whether it must needs pass first through the condition of Fibrin, cannot be distinctly affirmed; there is no positive evidence in support of either proposition; but the probabilities appear to the Author decidedly to favour the former view.

III. The great mass of the Gelatigenous tissues of the body, whose texture is *simply fibrous*, is also derived from the Albuminous element of the blood; but this passes through the intermediate condition of Fibrin, which may be regarded as a substance endowed with the power of self-development into a low form of organized structure, and therefore as having already undergone a vitalizing influence. There is no sufficient reason to believe, that Gelatin employed as food can ever be applied even to this purpose in the body; since all that we know of the *genesis* of the simple fibrous tissues, indicates that in assuming their characteristic structure, they pass through gradations similar to those which we witness in the production of the adventitious tissue of fibrinous exudations.

IV. When the death and disintegration of the tissues again bring their components under complete subjection to Chemical forces, an entirely different series of metamorphoses takes place, tending to degrade these components towards the condition of inorganic compounds. They would seem to resolve themselves into two classes of substances;—on the one hand, saccharine, oleaginous, and resinous matters, analogous to those of plants, in which carbon predominates;—on the other, a set of compounds peculiar to animals, of which nitrogen is the characteristic ingredient. From the albuminous constituent of muscle, for example, there is direct evidence that fat, sugar, and lactic acid may be generated on the one hand; on the other, creatine, and (probably through this creatine) urea, with the rest of the highly-azotized components of the urinary excretion. The sugar generated by the agency of the liver, from the products of the waste or disintegration of the system that are contained in the blood, seems to be at once employed in supporting the combustive process by which the animal heat is maintained. The fat may be directly applied to the same purpose, or may be stored-up in the cells of Adipose tissue for future use. The peculiar resinous acids of the bile, which are probably formed from the same source, appear to fulfil, in part, at least, a similar destination, after having been made subservient to other purposes. The lactic acid, chiefly generated in the substance of the muscles (probably by the metamorphosis of a saccharine compound, which may be looked-on as the immediate product of their disintegration), is in like manner destined to be carried-off by the respiratory process, though a part of it may first be rendered subservient to the digestive operation. But if the respiratory process should not be sufficiently active to remove these highly-carbonized compounds from the blood, we may find the lactic and hippuric acids in the urine, with the addition of carbonaceous pigmentary matter. On the other hand, the highly-azotized substances are destined for immediate elimination by the kidneys; their presence in the current of the circulation being so hurtful, that accumulation even in small amount might induce fatal results.

V. Besides the foregoing substances, there are doubtless others which have not been so carefully studied, and which are passed-off by distinct channels. Thus, we have no precise knowledge of those products of disintegration which are thrown-off by the skin; and the proper fæcal matter, which is undoubtedly derived from some excretion poured into the alimentary canal, rather than from putrescent changes in the residue of the substances which are passing through it, has not yet been made the subject of accurate examination.

VI. Where more alimentary matter is introduced into the blood, than is required for the *genesis* of living tissue, this probably undergoes the same decomposing changes, as do the effete matters that are set-free by the disintegration of the organized fabric. The saccharine and oleaginous matters are directly carried-off by the combustive process, only that portion being applied to the production of adipose tissue, which may not be required for the maintenance of the temperature of the body; whilst the albuminous and gelatinous appear to be resolved into the two classes of compounds already indicated, part of which are eliminated by the liver and lungs, the other part chiefly by the kidneys, but also by the skin and (its internal reflexion) the alimentary canal. It may here be mentioned, as affording positive evidence of the production of sugar from albuminous compounds within the living body, that it is found in the milk of Carnivorous animals, which have been for some time restricted to a diet of animal flesh.*—Our data are at present far too imperfect, to allow this series of metamorphoses to be definitely represented by the aid of formulæ; nevertheless there are certain general relations which have a real existence, and which may be appropriately indicated in this mode. The following are given by Prof. Liebig,† as examples of the transformations which *may* occur; it is to be observed, however, that some of the formulæ which he employs (op. cit. p. 437), differ from those in common use.

1 equiv. of Albumen with 10 equiv. of Water, contains the elements of 2 equiv. of Gelatin and 1 equiv. of Choleic (tauro-cholic) acid, thus—

$$\begin{array}{lrrrrr} & \text{C.} & \text{H.} & \text{N.} & \text{O.} & \text{S.} \end{array} \qquad \begin{array}{rrrrrl} \text{C.} & \text{H.} & \text{N.} & \text{O.} & \text{S.} & \end{array}$$

$$\left.\begin{array}{lrrrrr} 1\ \text{Albumen} = & 216 & 169 & 27 & 68 & 2 \\ 10\ \text{Water} \quad = & & 10 & & 10 & \\ \hline & 216 & 179 & 27 & 78 & 2 \end{array}\right\} = \left\{\begin{array}{rrrrrl} 164 & 134 & 26 & 64 & & = 2\ \text{Gelatin.} \\ 52 & 45 & 1 & 14 & 2 & = 1\ \text{Choleic acid.} \\ \hline 216 & 179 & 27 & 78 & 2 & \end{array}\right.$$

1 equiv. of Fibrin of Blood with 8 equiv. of Water, contains the elements of 1 equiv. of Gelatin and 1 equiv. of Albumen.

$$\begin{array}{lrrrrr} & \text{C.} & \text{H.} & \text{N.} & \text{O.} & \text{S.} \end{array} \qquad \begin{array}{rrrrrl} \text{C.} & \text{H.} & \text{N.} & \text{O.} & \text{S.} & \end{array}$$

$$\left.\begin{array}{lrrrrr} 1\ \text{Fibrin} = & 298 & 228 & 40 & 92 & 2 \\ 8\ \text{Water} \quad = & & 8 & & 8 & \\ \hline & 298 & 236 & 40 & 100 & 2 \end{array}\right\} = \left\{\begin{array}{rrrrrl} 216 & 169 & 27 & 68 & 2 & = 1\ \text{Albumen.} \\ 82 & 67 & 13 & 32 & & = 1\ \text{Gelatin.} \\ \hline 298 & 236 & 40 & 100 & 2 & \end{array}\right.$$

1 equiv. of Casein with 10 equiv. of Oxygen, contains the elements of 1 equiv. of Albumen and 1 equiv. of Chondrin.

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[*] This was at one time denied by Dumas; but the fact has been fully established by the researches of Bensch, who has also explained the reason of Dumas' failure to detect the presence of sugar. (See "Ann. der Chem. und Pharm." band lxi. p. 221).

[†] "Familiar Letters on Chemistry," p. 439.

$$\left.\begin{array}{lrrrrr} & \text{C.} & \text{H.} & \text{N.} & \text{O.} & \text{S.} \\ 1\ \text{Casein} & =288 & 228 & 36 & 90 & 2 \\ 10\ \text{Oxygen} & = & & & 10 & \\ \hline & 288 & 228 & 36 & 100 & 2 \end{array}\right\} = \left\{\begin{array}{rrrrrl} \text{C.} & \text{H.} & \text{N.} & \text{O.} & \text{S.} & \\ 216 & 169 & 27 & 68 & 2 & = 1\ \text{Albumen.} \\ 72 & 59 & 9 & 32 & & = 1\ \text{Chondrin.} \\ \hline 288 & 228 & 36 & 100 & 2 & \end{array}\right.$$

The three preceding formulæ represent such metamorphoses as may occur in the *genesis* of tissues; the following represent some of those which may take place in their *disintegration*, in which (it must be remembered) oxygen drawn from the air performs an important part.

1 equiv. of Albumen with 10 equiv. of Water and 56 equiv. of Oxygen, contains the elements of 1 equiv. of Choleic (tauro-cholic) acid, 2 equiv. of Cholic (glycho-cholic) acid, 12 equiv. of Urea, and 36 equiv. of Carbonic acid.

$$\left.\begin{array}{lrrrrr} & \text{C.} & \text{H.} & \text{N.} & \text{O.} & \text{S.} \\ 1\ \text{Albumen} & =216 & 169 & 27 & 68 & 2 \\ 10\ \text{Water} & = & 10 & & 10 & \\ 56\ \text{Oxygen} & = & & & 56 & \\ \hline & 216 & 179 & 27 & 134 & 2 \end{array}\right\} = \left\{\begin{array}{rrrrrl} \text{C.} & \text{H.} & \text{N.} & \text{O.} & \text{S.} & \\ 52 & 45 & 1 & 14 & 2 & = 1\ \text{Choleic acid.} \\ 104 & 86 & 2 & 24 & & = 2\ \text{Cholic acid.} \\ 24 & 48 & 24 & 24 & & = 12\ \text{Urea.} \\ 36 & & & 72 & & = 36\ \text{Carbonic acid.} \\ \hline 216 & 179 & 27 & 134 & 2 & \end{array}\right.$$

1 equiv. of Gelatin with 10 equiv. of Oxygen, contains the elements of 1 equiv. of Cholic (glyco-cholic) acid, 3 equiv. of Uric acid, and 12 equiv. of Water.

$$\left.\begin{array}{lrrrr} & \text{C.} & \text{H.} & \text{N.} & \text{O.} \\ 1\ \text{Gelatin} & =82 & 67 & 13 & 32 \\ 10\ \text{Oxygen} & = & & & 10 \\ \hline & 82 & 67 & 13 & 42 \end{array}\right\} = \left\{\begin{array}{rrrrl} \text{C.} & \text{H.} & \text{N.} & \text{O} & \\ 52 & 43 & 1 & 12 & = 1\ \text{Cholic acid.} \\ 30 & 12 & 12 & 18 & = 3\ \text{Uric acid.} \\ & 12 & & 12 & = 12\ \text{Water.} \\ \hline 82 & 67 & 13 & 42 & \end{array}\right.$$

1 equiv. of Chondrin contains the elements of one Cholic (glyco-cholic) acid, 2 Uric acid, and 8 Water.

$$\left.\begin{array}{lrrrr} & \text{C.} & \text{H.} & \text{N.} & \text{O.} \\ 1\ \text{Chondrin} & =72 & 59 & 9 & 32 \end{array}\right\} = \left\{\begin{array}{rrrrl} \text{C.} & \text{H.} & \text{N.} & \text{O.} & \\ 52 & 43 & 1 & 12 & = 1\ \text{Cholic acid.} \\ 20 & 8 & 8 & 12 & = 2\ \text{Uric acid.} \\ & 8 & & 8 & = 8\ \text{Water.} \\ \hline 72 & 59 & 9 & 32 & \end{array}\right.$$

Now although it must be admitted that, by a dextrous management of formulæ, almost any kind of transformation may be effected *on paper*, yet the above coincidences are so remarkable in themselves, and are so closely accordant with phenomena of whose occurrence we have independent evidence, that it seems hardly just to regard them as merely fortuitous.

VII. The Inorganic acids, bases, and saline compounds, which properly rank as constituents of the body, are for the most part applied to its construction in the forms in which they were introduced from the food; and they reappear under the same forms in the excretions. But new compounds are also produced during the progress of the metamorphic changes already referred-to. Thus, a portion of the Sulphur taken-in as a constituent of albuminous food, seems to be oxidised in the final disintegration of the tissues by which that albumen was appropriated, and is converted into sulphuric acid; a part, however, still remaining unoxidised, and passing off in that state both by the bile and the urine. So, again, if Phosphorus (as such) be a constituent of the protein-compounds, or be united with fatty matters, it must undergo a similar oxidation within the system; as it scarcely ever presents itself in the excretions under any other form than that of phosphoric acid. On the other hand, by the oxidation of various organic acids largely contained in vegetable food, their alkaline bases are reduced to the state of carbonates, so as to be ready to combine with any of the stronger acids that may be present in the system; and ammonia seems also to be generated *de novo*. Thus a supply of bases is prepared, ready to neutralize not merely the acids whose mode of production has just been described, but also the uric, hippuric, and lactic acids which are generated within the body, and which do not readily pass-off from it except in combination with bases; and according as the proportion of these bases is equivalent to that of the acids, exceeds it, or is exceeded by it, will the urine be neutral, alkaline, or acid.—When mineral substances, whose presence is superfluous or noxious, are introduced into the body, an effort is usually made for their elimination, by some of the excretory organs; most commonly by the kidneys.

390. It has been shown (§ 345) that in the Nutrition of the parts concerned in the maintenance of Organic life alone, the quantity of new tissue produced (the requisite amount of formative power being supplied) depends chiefly upon the quantity of material specially adapted for its generation. But in the case of the tissues which minister to the Animal functions, a different rule seems to hold good; for in these we find that the activity of reparation is dependent upon the degree of previous waste or disintegration, caused by the performance of their peculiar operations; so that, if they be kept in complete inactivity, no nutritive changes can take place in them, notwithstanding the greatest abundance of their respective *pabula*, and degeneration immediately commences; whilst, if their functions be performed with unusual energy, so that an increased amount of 'waste' takes place, this waste is more than repaired by the nutritive activity of the part (provided that a sufficient amount of duly-prepared material be supplied), and a positive *increase* of its substance, with a like increase of functional power, is the result. It is a very remarkable circumstance, that the nutrition of *bones*, at least in those situations in which they serve to afford fixed points of attachment to muscles, rather than to support and protect the softer parts, is closely related to the development of the muscles; so that when this is augmented by continued activity, the bones become stronger, and their prominences and ridges more decided; whilst if it be checked by disuse, the nutrition of the bone also is impaired, and its bulk speedily diminishes.*

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* Thus Dr. John Reid found that the relative weights of the Bones and Muscles of the two hind-legs of a rabbit, from which a portion of the sciatic nerve on one side had been removed seven weeks before, so as entirely to paralyze the limb, were as follows.

	Sound limb.	Paralyzed limb.
Muscles	327 grains	170 grains.
Tibia and Fibula	89 grains	81 grains.

There was an obvious difference, also, in the ultimate structure of the muscles of the two limbs; for the fibres of the paralyzed muscles were considerably smaller than those of the other side, exhibited the longitudinal and transverse striæ much less distinctly, and had a shrivelled appearance. ("Physiological, Pathological, and Anatomical Researches," p. 10.)

391. Thus the condition of nutritive activity in the tissues which are the instruments of the Animal functions, is as strikingly opposed to that which prevails in the part of the organism appropriated to the Vegetative functions, as are the conditions under which those functions are respectively performed. For, as we have seen, *Vegetative* activity of every kind is entirely *constructive;* and its conditions are merely (1) the supply of organisable matter, and (2) the requisite organising force. On the other hand, *Animal* activity is in its essential nature *destructive;* and its conditions involve the re-conversion of organised tissue into the inorganic state. But, in some mode not yet understood, the performance of this *de*structive operation excites a corresponding exertion of the *con*structive; and the tissues are renewed or even augmented. The explanation may perhaps lie in the fact, that the exercise of the endowments of the Nervous and Muscular tissues, which depends upon conditions external to themselves,* itself becomes a means of determining an increased afflux of blood, to them, on the principles already laid-down (§ 252); and it is on the increase of vegetative activity which thus takes place, that the augmented nutrition seems to depend. On the other hand, when these tissues are not called into action, the circulation through them becomes extremely languid, and their nutrition suffers accordingly.

392. In addition to the foregoing peculiarities, it is to be remarked that the activity of nutrition among higher Animals varies greatly in proportion to the *age* of the individual. Among Plants, one part of the fabric may die, whilst another is vigorously growing and extending itself, the two having no relation of mutual dependence; and the same may happen among Zoophytes. But we find, as we ascend the Animal series, that as the individual parts become more and more intimately dependent upon one another, the nutritive activity of each is more and more closely related to that of the remainder, and consequently to that of the organism at large. Moreover, we find that *growth* consists less in mere external addition to the parts already formed (as it does for the most part in Plants), but more and more in interstitial enlargement; and this involves a continual remodelling of the entire fabric. Thus all the tissues, even those most consolidated, are undergoing continual changes in the young animal; and it would seem as if the duration of their component parts is much less than in more advanced life, so that disintegration and renewal more rapidly succeed each other (§ 117). Here, as elsewhere, we find that *duration* and *functional activity* are in the inverse ratio to each other.

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* The activity of Muscle must be called forth by the stimulus of innervation, or by other excitants immediately applied to itself. That of the *afferent* portion of the Nervous substance is entirely dependent upon the reception of impressions from without, so that if these be withheld it remains in a state of torpor, and its nutrition is proportionably affected,—as we see in the case of the eye, when the access of light to the retina is completely prevented by opacity of the cornea. In like manner, the activity of the central organs is dependent upon the excitement which they receive through the afferent nerves, or from mental operations; and thus we find that a continuance of intellectual exertion, if not too severe, tends to augment the nutrition of the brain. And the activity of the *efferent* portion of the nervous system is entirely dependent upon that of the central organs, so that the nutrition of any part of it ceases, as soon as it is separated from them. But it is a remarkable circumstance, first clearly ascertained by Dr. Waller, that if the connection of the sensory nerves with the central organs be interrupted, so that they cannot propagate onwards the impression they have received, their nutrition is immediately impaired. ("Philosophical Transactions," 1850, Part II.)

The dull perceptions, and slow and feeble movements, of the aged individual, are in no less striking contrast with the acute sensibility, and the rapid and vigorous muscular actions, of the child, than is the sluggishness of the interstitial changes in the former, as compared with their energy and activity in the latter. Hence it may be stated as a general fact, that the vital activity of the component parts of the organism diminishes with the prolongation of the general life of the whole.

393. That the function of Animal Nutrition is capable of being considerably *modified* by the influence of the Nervous system, cannot be doubted by any one who duly considers the facts which have been brought to light by experiment and observation. But still there appears to be no sufficient reason for regarding the ordinary Nutritive operations as in themselves necessarily *dependent* upon Nervous agency (§ 97). In fact, the results of injury to the nerves of a part seem to be exerted rather in a disturbance or perversion, than in an actual suspension of them. And seeing as we do, that active nutrition takes place in the embryo, long before nerves have been developed, and that it goes-on in parts (*e. g.* cartilage) into which it may be said with certainty that no nerves enter, we seem to have full confirmation of the inference, which rests upon the essential conformity between the processes of Animal and Vegetable Nutrition,—that in the one case, as in the other, the operation is effected by the formative powers of the part itself, exerted upon the plastic material supplied to it; but that these, in the Animal, are modified and directed by Nervous agency, in such a manner as to harmonise them with each other, and with the general requirements of its organism.

CHAPTER IX.

OF SECRETION AND EXCRETION.

1. *General Considerations.*

394. The parallel between the Vegetable and Animal kingdoms, which has hitherto been so close, fails us when we arrive at this department of the enquiry; for the conditions of Vegetable existence do not require that provision for the maintenance of the purity of the nutritive fluid, by the removal of effete matters, which becomes the most constant and urgent necessity of Animal life. It would seem as if all the nutritive material assimilated by the leaves of Plants, is applied to their growth and development, or is stored-up as a provision for future operations of the same kind; and the supply is so exactly proportioned to the demand (§ 346), that there is seldom any unappropriated residue of assimilated matter left to become injurious by its superfluity and by its tendency to decomposition. Moreover, the parts which have fulfilled their purposes in the system, and whose term of life is expired (such as the leaves and flowers), are cast off *en masse;* their ultimate decay, in which they return to the state of simple binary compounds, takes place after their

separation; and no such interstitial death and decomposition occur in the regular progress of Vegetable life, as we have seen to be necessary conditions of Animal activity. There is nothing, then, save Carbonic acid and Water, which needs to be cast-out of the Vegetable organism; and for the elimination of these, we have found a special provision to be made.—In the Animal, on the other hand, there are numerous modes in which the Circulating fluid may be rendered impure. In the first place, a larger amount of nutriment may be introduced into the blood, than the Nutritive operations can appropriate: for we have just seen that the formative energy of those Nervo-muscular tissues, which make-up by far the largest proportion of the bodies of the higher animals, has no relation whatever to the supply of food, but depends upon the exercise to which they have been subjected; so that, unless the amount of food ingested be proportioned to this, there must remain a superfluity which soon becomes injurious by decomposition, its highly-azotised nature rendering it peculiarly liable to undergo this change, at the elevated temperature of warm-blooded animals. Further, it seems scarcely possible that the varied demands which are made upon the nutritive fluid of higher animals, for the supply of the requisite components of the several tissues, can be so accurately adjusted under all circumstances, as not to leave some residue incapable of further use, and therefore unsuitable to be retained. But the great and constant occasion for the excretory operations, undoubtedly arises from the disintegration, to which, as so frequently mentioned, the whole apparatus of Animal life is subject as the very condition of its vital activity; and therefore the demand for their performance will vary with the degree of that activity. All that has been already said on this point under another head (§§ 277, 278), is equally applicable here. So urgent is the necessity for this process, that, as Dr. Marshall Hall has justly remarked, the functions of *egestion* are more immediately necessary to the maintenance of Animal life, than are those of *ingestion*. This will more fully appear hereafter.

395. But besides that separation of effete matters from the blood, for the purpose of maintaining its purity, which is usually distinguished as *Excretion*, we find that certain products are elaborated from it for special purposes in the economy; and it is to the process by which this is accomplished, that the term *Secretion* in its more restricted sense is applicable. But even this has scarcely any parallel in the Vegetable kingdom. For although there is a large class of substances which are commonly designated as 'Vegetable Secretions,' yet these are not poured-out upon the surface nor into the cavities of the Plant, but are stored-up in its constituent cells, of which they form the characteristic contents; and thus they bear the same relation to it, as the oleaginous contents of the fat-cells, or the calcareous deposit in the cells of shells, &c., bear to the Animal organism (§ 359). We shall presently see, however, that the production of the true Secretions and even of the Excretions of Animals, is a process which is referable to the same general category as Nutrition; the separation of the several components of each, from the blood, being effected by the development of cells, to which they form the appropriate pabulum (§ 398, 399).

2. *Secretion in Vegetables.*

396. It might seem almost superfluous to add anything under this head, to what has been just said, as to the absence of any true secreting or excreting process in Plants. But there are certain doctrines current upon this subject, to which it seems necessary to make more particular allusion.—The nearest approach to a true *Excretion* seems to be presented by those cases, in which peculiar organic compounds are exuded from the surface; as honey in flowers, wax upon leaves and fruits, gums and gum-resins upon bark, &c. In these and other similar instances, however, the exudation appears chiefly to result from the superabundance of the product in the subjacent tissues, and is not to be considered in any other light than as relieving their distension. It may be subservient at the same time, however, to some secondary purpose; thus the honey of the flowers is attractive to insects, whose services in the act of fertilization are frequently important, and sometimes absolutely essential. And this, with the acrid fluids secreted in the so-called 'glands,' or agglomerations of cells, at the base of the hairs of the Nettle, &c., may be regarded as the nearest approximations exhibited by Plants to the true *Secretions* of Animals.

397. It has been imagined that Plants have the power of throwing-off from their roots, substances injurious to their economy; and the matters thus separated have been regarded as real Excretions. Thus it was found by Bonnet, that if a rapidly-growing plant have its roots divided into two bundles, and one of these be introduced into a solution of some saline substance which it will absorb, whilst the other is immersed in pure water, the latter fluid will be found after a few days to have received a certain impregnation from the former; apparently showing that the salt must have been taken-up through one set of roots, and cast out again through the other. But this inference is open to the fallacy, that the saline substance may have passed from one vessel to the other by capillary attraction merely, along the exterior of the roots.—Again, it has been stated by Macaire, that if a *Leguminous* plant be placed in distilled water, the fluid will be found in a few days strongly impregnated with mucilaginous matter, which it has derived from the roots immersed in it; so the *Cichoraceæ* and *Papaveraceæ* are said to exude a large quantity of a brownish bitter matter analogous to opium; *Euphorbiaceæ*, an acrid gummy-resinous matter; and so on,—the substances exuded being in all instances those which are characteristic of the proper juices of the plants which furnish them. It has been rendered very doubtful, however, by the subsequent experiments of Braconnot, Boussingault, and others,* whether any such exudation takes place when the roots are uninjured; and if it have a real existence, it is probably to be regarded less an excretion, than as a simple act of *exosmose*, necessarily connected with the endosmose by which water is taken-up into the organism (§ 177). The supposed existence of such exudations has been thought to account for the fact, that the growth of particular species of plants favours the subsequent development of other kinds; whilst there are other species, whose growth seems to leave the soil in a

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* See Mohl "On the Vegetable Cell," translated by Henfrey, p. 98.

much worse condition than before. But there can be little doubt that much of the latter result is to be attributed to the removal of particular ingredients from the soil, which render it less fitting to sustain the continued growth of its own kind, whilst it may still be capable of affording the requisite support to such as need some different materials; and it is probably in this manner that we are to explain the well-known fact in forestry, that where a wood principally composed of one species of timber-trees has been cleared by fire or otherwise, the trees which spring-up spontaneously and supply the place of the former growth, are for the most part of a different species; and the success of the 'rotation of crops' in agriculture seems chiefly attributable to the same cause. This, however, may not be all; for it is well known that the soil is more benefited by the growth of a crop of certain Leguminous plants, such as Trefoil, than it would be by lying absolutely fallow; and this can scarcely be due to anything else, than its impregnation with gummy exudations from the roots of these plants. On the other hand, there are exudations which are positively injurious; this has been proved to be the case with tannin, which is given-off by the roots of the Oak, and which, even in very minute proportion, destroys the vitality of the growing tissues of the spongioles of other plants; thus affording an explanation of the well-known fact, that trees transplanted into a soil in which oaks have previously grown, seldom flourish, and generally die. And it seems not unlikely, too, that Poppies and other 'rank' weeds do more damage by communicating narcotic exudations to the soil, which deaden the vital powers of other plants growing in it, than by any exhaustive influence exerted by them.

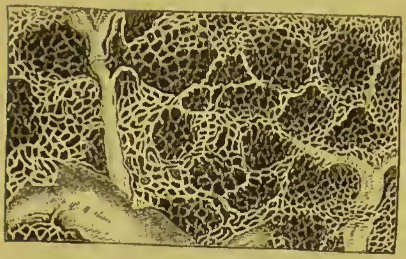
3. *Secretion in Animals.*

398. We have seen that, in the process of Animal Nutrition, the circulating current not only *deposits* the materials which are required for the renovation of the solid tissues; but also *takes back* the substances which are produced by the decay of these, and which are destined to be thrown-off from the body. We have also seen that it supplies the materials of certain fluids, which are separated from it to effect various purposes in the economy;—such as the Salivary and Gastric secretions, which have for their office to assist in the reduction of the food. Now the process by which the fluids of the latter kind are separated from the Blood, is identical in character with that by which the products of decay are eliminated from it; and the structure of the organs concerned in the two is essentially the same. Hence both processes are commonly included under the general term *Secretion;* which, considered in its most general point of view, may be applied to *every* act, by which substances of any kind are *separated* from the blood; but which is usually restricted to those cases, in which the substances withdrawn are not destined either to be restored again to the circulating current (as in Assimilation), or to form part of the textures of the living fabric (as in Nutrition); and in which the separated product has a liquid or more rarely a solid form, and not a gaseous (as in Respiration). Viewed under this limitation, the essential character of the true *Secreting* operation seems to consist,—not in the nature of the action itself, for this is iden-

tical with those of Assimilation and Nutrition, being a process of cell-growth,—but in the position in which the cells are developed, and the mode in which the products of their action are afterwards disposed-of. Thus the cells at the extremities of the intestinal villi (§ 182), the cells of which the adipose tissue is made-up, and the cells of which the greater part of the substance of the liver is formed (§ 409), all have an attraction for fatty matter; and draw it from the neighbouring fluids, at the expense of which they are developed, to store it up in their own cavities. But the cells of the first kind deliver the materials which they have drawn-in, to the absorbent vessels, which introduce them into the circulating current:—those of the second kind, which are more permanent in their character, retain their contents, so as to form part of the ordinary tissues of the body, until they are required to give them up;—whilst the cells of the third class cast forth *their* contents into the hepatic ducts, by which they are carried into the intestinal canal, whence a portion of them at least is directly conveyed out of the body. It is, then, in the *position* of the Secreting cells,—which causes the product of their action to be delivered upon a *free surface,* communicating, more or less directly, with an external outlet,—that their distinctive character depends. All the proper *Secretions* are thus poured-out either upon the exterior of the body, or into cavities provided with orifices that lead to it. Thus we have seen that a very large quantity of fluid, containing a considerable quantity of solid matter, of which it is desirable that the system should be freed, is carried-off from the Cutaneous surface. Another most important secretion, containing a large quantity of solid matter, and serving also to regulate the quantity of fluid in the system,—namely, the Urinary,—is set free by a channel expressly adapted to convey it directly out of the body. The same may be said of the Mammary secretion; which is separated from the blood, not to preserve *its* purity, nor to answer any purpose in the economy of the individual, but to afford nutriment to another being. And of the matters secreted by the very numerous glandulæ and follicles situated in the walls of the Intestinal canal, a great part seem to be poured into it for no other purpose, than that they may be carried out of the body by the readiest channel.

399. The cells covering the simple membranes that form the free surfaces of the body, whether external or internal, are all entitled to be regarded as *secreting* cells; since they separate various products from the blood, which are not again to be returned to it. But the secreting action of some of these seems to have for its object the *protection* of the surface: thus the Epidermic cells of the skin secrete a horny matter, by which density and firmness are imparted to the cuticle; whilst by the Epithelial cells of the mucous membranes of the alimentary canal and of other parts, their protective mucus seems to be elaborated. But in general we find that special organs, termed *Glands,* are set-apart for the production of the chief secretions; and we have now to consider the essential structure of these organs, and the mode of their operation.—An ordinary Gland may be said to consist of a closely-packed collection of follicles (Fig. 173), all of which open into a common channel, by which the product of the glandular action is collected and delivered. The follicles contain the secreting cells in their cavities; whilst their exterior is in contact with a

Fig. 169.

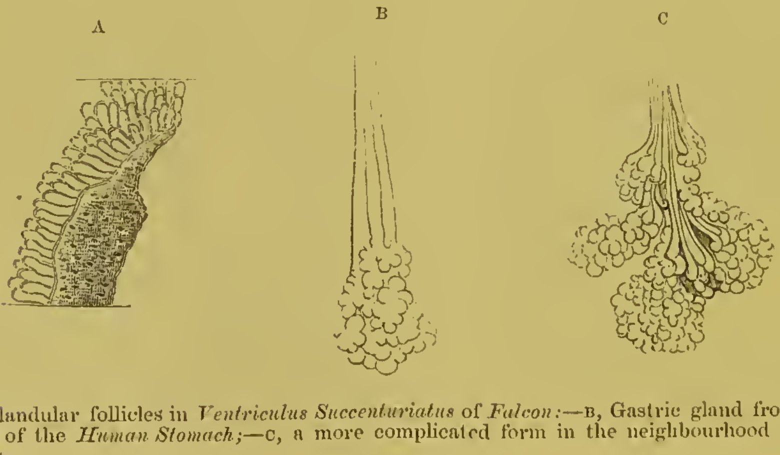


Capillary network around the follicles of *Parotid Gland.*

network of blood-vessels, from which the cells draw the materials of their growth and development (Fig. 169). In any one of the higher animals, we may trace-out a series of progressive stages of complexity, in the various glands included within their fabric; and in following any one of the glands that attain the highest degree of development (such as the Liver or Kidney), through the ascending scale of the animal series, we shall be able to trace a very similar gradation from its simplest to its most complex form. Hence we see that there can be nothing in the *form* or *disposition* of the components of the glandular structure, which can have any influence upon the character of the secretion it elaborates; since the very same product,—*i. e.* the Bile, or the Urine,—is found to issue from nearly every variety of secreting structure, as we trace it through the different groups of the Animal kingdom. The peculiar power by which one organ separates from the blood the elements of the Bile, and another the elements of the Urine, whilst a third merely seems to draw-off a certain amount of its albuminous and saline constituents, is obviously the attribute of the ultimate secreting cells, which are the real agents in the secreting process. *Why* one set of cells should secrete bile, another urea, and so on, we do not know; but we are equally ignorant of the determining cause which makes one set of cells convert itself into Bone, another into Muscle, and so on. This variety in the endowments of the cells, by whose aggregation and conversion the fabric of the higher Animals is made-up, is a fact which we cannot explain, and which must be regarded (for the present, at least,) as one of the 'ultimate facts' of Physiological Science.

400. Passing-by the extended membranous surfaces, and the protective or secreting cells with which they are covered, we find that the simplest form of a secreting organ is composed of an *inversion* of that surface into follicles, which discharge their contents upon it by separate orifices. Of this we have a characteristic example in the *gastric* follicles,

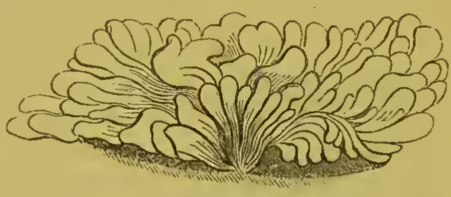
Fig. 170.



A, Glandular follicles in *Ventriculus Succenturiatus* of *Falcon*:—B, Gastric gland from the middle of the *Human Stomach*;—C, a more complicated form in the neighbourhood of the pylorus.

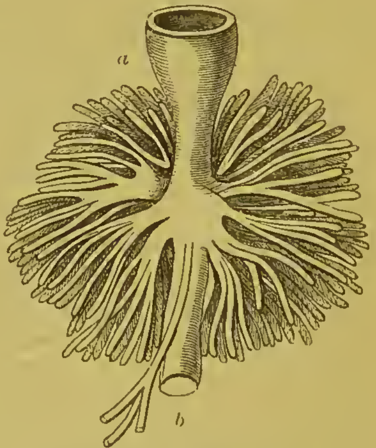
even among the higher animals; the apparatus for the secretion of the Gastric fluid never attaining any higher condition, than that of a series of distinct follicles, lodged in the walls of the stomach, and pouring their products into its cavity by separate apertures. In Fig. 170, A, is represented a portion of the 'ventriculus succenturiatus' of a Falcon, in which the simplest form of such follicles is seen. A somewhat more complex condition is seen in some of the Gastric follicles of the Human stomach (B, C); the surface of each follicle being further extended by a sort of doubling upon itself, so as to form the commencement of secondary follicles, which open out of the cavity of the primary one.—Now a condition of this kind is common to *all* glands, in the first stage of their evolution; and in this stage we meet with them, either by examining them in the lowest animals in which they present themselves, or by looking to an early period of their embryonic development in the highest. Thus, for example, the *Liver* consists, in the lowest Mollusca, of a series of isolated follicles, lodged in the walls of the stomach, and pouring their product into its cavity by separate orifices; these follicles being recognised as constituting a biliary apparatus, by the colour of their secretion. And in the Chick, at an early period of incubation, the condition of the Liver is essentially the same with the preceding; for it consists of a cluster of isolated follicles, not lodged in the walls of the intestine, but clustered round a sort of bud or diverticulum of the intestinal tube, which is the first condition of the hepatic duct, and into which they discharge themselves (Fig. 180). So, again, the *Mammary Gland* presents an equally simple structure (Fig. 171) in that lowest type of the Mammalian class, the *Ornithorhyncus;* for it consists of nothing else than a cluster of cæcal follicles, discharging their contents by separate orifices upon the surface of the mammary areola. And in like manner, the *Pancreas* makes its appearance in many osseous Fishes, in the condition of a group of large cæca (Fig. 126, 3), that seem like prolongations of the stomach into which they freely open; whilst in the Octopus, this gland is represented by a single such appendage, which is prolonged and specially convoluted. A transition towards a higher form is seen in the Cod, whose pancreas is composed of a numerous group of prolonged cæcal follicles, clustered round the commencement of the intestinal canal, and partly coalescing with each other before they enter it (Fig. 172). Thus it may be stated as a general rule, that every gland presents itself under this most elementary state, alike in the lowest grade of the animal series in which it is first

Fig. 171.



Mammary Gland of *Ornithorhyncus.*

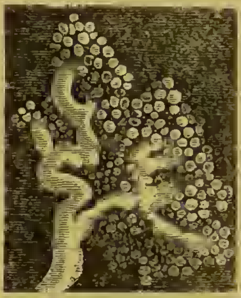
Fig. 172.



Rudimentary Pancreas from *Cod:*— *a,* pyloric extremity of stomach; *b,* intestine.

traceable, and at its earliest appearance in the embryo of the higher.—The next grade of complexity is seen, where a cluster of the ultimate follicles open into one common duct, which discharges their product by a single outlet; a single gland often containing a number of such clusters, and having, therefore, several excretory ducts. A good example of such a condition, in which the clusters remain isolated from one another, is seen in the Meibomian glands of the eyelid; each of which consists of a double row of follicles, set upon a long straight duct, that receives the products of their secreting action, and pours them out upon the edge of the eyelid. And of the more complex form, in which a number of such clusters are bound-together in one glandular mass, we have an illustration in the accessory glands of the genital apparatus in several animals, which discharge their secretion into the urethra by numerous outlets; in the pancreas of the higher Cartilaginous Fishes; or in the mammary glands of Mammalia in general, the ultimate follicles of which are clustered upon ducts that coalesce to a considerable extent, though continuing to form several distinct trunks even to their termination. Such glands may be subdivided, therefore, into *glandulæ* or *lobules*, that remain entirely distinct from each other.—In the highest form of Gland, however, all the ducts unite, so as to form a single canal, which conveys away the products of the secreting action of the entire mass. This is the condition under which we find the Liver to exist in most of the higher animals; also the Pancreas, the Parotid Gland, and many others. In some of these cases, we may still separate the gland into numerous distinct lobules, which are clustered upon the excretory duct and its branches, like grapes upon a stalk (Fig. 173); in others, however, the branches of the excretory duct do not confine themselves to *ramifying*, but *inosculate* so as to form a network, which passes through the whole substance of the gland, and which connects together its different parts, so as to render the division into lobules less distinct. This seems to be the case in regard to the Liver of the higher Vertebrata.

Fig. 173.



Lobule of Parotid Gland of *Human Infant*, filled with mercury; magnified 50 diameters.

401. Whatever degree of complexity, however, prevails in the general arrangement of the elements of the secretory Glands in higher animals, these elements are themselves everywhere the same; consisting of *follicles* or *tubuli* that enclose the real secreting cells (Figs. 174 and 175). Now from the history of the development of Glands in general, it appears that the *follicles* may be considered as primary cells; and that the *secreting* cells are secondarily developed in their interior, from the nuclei or germinal spots on the walls of the first. It has been pointed out by Prof. Goodsir,* that the continued development and decay of the glandular structure, in other words, the elaboration of its secretion, may take place in two different modes:—In one class of Glands, the 'primary' cell, having begun to develope new cells in its interior, gives way at one point, and bursts into the excretory duct, so as to become an open follicle, instead

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* "Anatomical and Pathological Observations," chap. xv.

of a closed cell: its contained or 'secondary' cells, in the progress of their own growth, draw into themselves the matter to be eliminated from the blood, and having attained their full term of life, burst or liquefy, so as to discharge their contents into the cavity of the follicle, whence they pass by its open orifice into the excretory duct: and a continual new production of secondary cells takes place from the germinal spot, or nucleus, at the extremity of the follicle, which is here a permanent structure. In this form of gland, we may frequently observe the secreting cells existing in various stages of development within a single follicle; their size increasing, and the character of their contents becoming more distinct, in proportion to their distance from the germinal spot (which is at the blind termination of the follicle), and their consequent proximity to the outlet (Fig. 175). In some varieties of such glands, however, (as in the greatly prolonged follicles, or tubuli uriniferi, of the kidney) the production of new cells does not take place from a single germinal spot at the extremity of the follicle, but from a number of points scattered through its entire length.—In the second type of Glandular structures, the 'primary' cell does not remain as a permanent follicle; but, having come to maturity and formed a connection with the excretory duct, it discharges its entire contents into the latter, and then shrivels-up and disappears, to be replaced by newly-developed follicles. In each primary cell of a gland formed upon this type, we find all its 'secondary' or secreting cells at nearly the same grade of development; but the different primary cells, of which the parenchyma of the gland is composed, are in very different stages of growth at any one period, some having discharged their contents and being in progress of disappearance, whilst others are just arriving at maturity and connecting themselves with the excretory duct; others exhibiting an earlier degree of development of the secondary cells; others presenting the latter in their incipient condition; whilst others are themselves just starting into existence, and as yet exhibit no traces of a secondary brood.—The former seems to be the usual type of the ordinary Secreting Glands; the latter is chiefly, if not solely, to be met-with in the Spermatic glands.

402. The purposes answered by the function of *Secretion* we have seen to be two-fold: namely, the separation of some material from the circulating fluid, which would be injurious to the welfare of the system if retained in it; and the elaboration of a product, which is destined to some other use in the economy. Now it is probable that in almost every act of secretion, both these purposes are in some degree served: the blood being freed from some ingredient whose accumulation would be superfluous, if not more positively injurious; and the matter separated having some secondary purpose to answer. Thus, whilst Biliary matter becomes a positive poison if it be retained in the blood, it contributes, when poured into the duodenum, to complete the digestive process, and to prepare the nutrient contents of the intestinal canal for absorption. So, again, the Cutaneous exhalation not only removes the superfluous water of the blood, but is one of the chief means of regulating the temperature of the body. And even the Urine, which seems to be eliminated merely for the removal of the products of the disintegration of the tissues from the circulating current, is sometimes made to serve an additional purpose; its acridity, or its peculiarly offensive odour (increased under the influence of

terror), frequently rendering it an effectual means of defence. On the other hand, the secretions which are separated from the blood for the purpose of discharging some important office in the economy, usually, if not always, contain some substances whose retention in the blood would be injurious, and which are therefore advantageously got rid of through this channel. Thus the Salivary, the Gastric, and the Pancreatic fluids, all contain an animal principle nearly allied to albumen; but this principle seems to be in a state of change, or of incipient decomposition; and it would not seem improbable, that whilst this very condition renders the albuminous matter useful in promoting the reduction of the aliment, it renders it unfit to be retained in the circulating current.—It is impossible, therefore, to divide the secreted products strictly, as some Physiologists have attempted to do, into the *excrementitious* and the *recrementitious;* that is, into those which are purely excretory in their character, and those which are subservient to further uses in the economy; since most, if not all of them, partake more or less of both characters. Still it is convenient to group them, for practical purposes, according to the *predominance* of one or other of the objects first mentioned; those being regarded as *Excretions,* in which the depuration of the blood is manifestly the chief end, any other purpose being rendered subservient to this; and those being ranked as *Secretions,* in which the ulterior purpose of the separated fluid would seem to be the principal occasion of its production.

403. Another classification has been proposed, of which the foundation is the degree of resemblance which the secreted products bear to the normal constituents of the Blood: those being associated into the first group, in which the characteristic ingredients are altogether unlike those of the nutritive fluid; whilst a second group is formed of those, whose elements seem nearly allied to the components of the blood. This classification is, in fact, almost identical with the preceding; for, as a general rule, all the cases in which the secreted products are very unlike the constituents of the blood, are those in which they are most directly and speedily removed from the body; whilst those in which they serve some ulterior purpose, are for the most part also those, whose elements differ least from the components of the blood.—The products of the first class may be said to have their immediate origin in the disintegration of the tissues; and we find the amount in which they are generated, to be in close relation to the operation of the various causes which tend to increase or to diminish that disintegration (§§ 113—117). They all act as *poisons,* if retained within the system and allowed to accumulate even for a short time; and after their excretion, they speedily resolve themselves into simple combinations of inorganic elements. This is the case, for example, with Urea, Biliary matter, and the putrescent portion of the Fæces; all of which may be regarded as the products of the metamorphosis of the tissues, on their way towards their restoration to the Inorganic universe (§ 389, IV); and it would seem to be *because* they have undergone this complete metamorphosis, that their presence in the circulating current is not only useless but injurious. We may consider that portion of the carbonic acid thrown-off by Respiration, which is the result of the disintegration of the tissues (§ 278), as the most important of these excretory products, being the one whose briefest accumulation gives rise to the most pernicious results; but the accumulation of biliary matter or

of urea, caused by the *complete* stoppage of the hepatic or renal excretions, usually proves fatal in from one to two days. Of the products of the first class it may be said, further, that many of them may be detected in the circulating blood, on account of their marked dissimilarity in chemical properties to its other constituents; though their quantity is normally extremely minute, since they are eliminated almost immediately that they are generated. But if any such secretory operation be checked, then the product which it is destined to remove, speedily makes its presence apparent in the blood; being not only detectable by chemical analysis, but also recognisable by the symptoms of poisoning to which it gives rise.—On the other hand, the products of the second class seem to be supplied rather from the materials of the blood itself, than from the disintegration of the tissues; and usually bear such a close relation to the normal constituents of the circulating fluid, as not to be distinguishable from them. Such are the elements of the Salivary, Gastric, Pancreatic, Lachrymal, and Mammary secretions. Hence, when these secretions are checked, the consequences are more apparent in the suspension of the function to which they are especially subservient, than in that general disorder of the system which indicates a contamination of the blood.

404. As it would be quite foreign to the purpose of this Treatise, to enter into a comparative examination of all the Secreting structures which present themselves in the different parts of the Animal series, it will be advantageous to restrict ourselves for the most part to two sets of organs—the Biliary and Urinary,—being those which are most generally distributed, and which present themselves under the greatest variety of forms and conditions. In the examination of these, we shall find ample illustration of the great principles of *specialisation* and *concentration* already so frequently referred-to; and shall also meet with some remarkable examples of that interchange of function, which occasionally takes place even in the most complex organisms.

405. *The Liver, and the Secretion of Bile.*—There are few animals possessed of a distinct digestive cavity, in which some traces of a biliary apparatus (recognizable by the colour of its secretion) cannot be distinguished. Thus in the *Hydraform Polypes*, cells containing a yellowish-brown matter may occasionally be seen in the lining of the stomach, into the cavity of which they probably discharge their contents, by the rupture or solution of their own walls.* Secreting cells of a similar kind are more distinctly seen in furrows formed by duplicatures of the lining membrane of the stomach of the *Actinia* (Fig. 35). In the *Laguncula* and other *Bryozoa* (Fig. 49), very distinct spots may be observed in the parietes of the stomach, which seem to be composed of clusters of biliary cells contained within follicles; and during digestion, the contents of the stomach are seen to be tinged with a rich yellow-brown hue, derived from the matter discharged from these follicles. In the *Earthworm*, again, the large annulated alimentary canal is completely encased in a flocculent external coating, which consists of a mass of minute flask-shaped follicles filled with cells; and several of these coalesce to discharge their contents by a common orifice into the digestive cavity.—Passing a little higher, as well in the Radiated, as in the Articulated and

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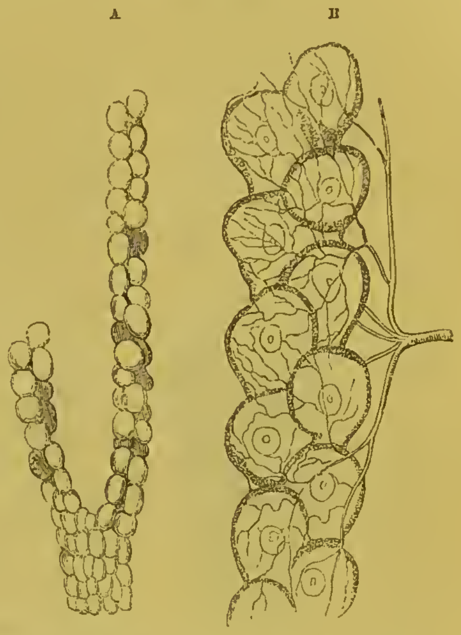
* See Prof. Allman 'On Cordylophora,' in "Philos. Transact." 1853, p. 370.

Molluscous groups, we find the hepatic cells clustering, not immediately around the digestive stomach, but around cæcal prolongations of this, which thus present us with the first approximation to the condition of the separate glandular mass, which we meet-with in the higher animals. Thus in the *Asterias* (Fig. 37), the radiating extensions of the stomach have their walls dilated into numerous culs-de-sac; and these are lined with large glandular cells, whose colour and aspect indicate their hepatic character. So in the *Leech* and many other *Annelida*, whose digestive cavity is more or less sacculated (Fig. 103), the walls of these sacculi are covered with biliary cells, as are also, although in a less degree, those of the central canal. In the *Pycnogonidæ*, again, the only trace of hepatic organs is to be found in the biliary cells, which are dispersed through the walls of the cæca prolonged into their limbs (Fig. 105); and it is apparently in the same diffused condition, that the biliary apparatus exists in the *Acarida* (§ 54). The most remarkable example of this type of structure in the Molluscous series, is presented by certain of the *Nudibranchiate* Gasteropods, in which, notwithstanding the high development which the liver attains in most other orders of the class, it is reduced to the condition of clusters of simple cells arranged round cæcal prolongations of the stomach. In the *Eolis* (Fig. 104) and its allies, the stomach gives-off on either side a number of branches, which usually re-divide, and then give-off smaller tubes, which are continued into the numerous papillæ that clothe the dorsal surface of these animals, and are subservient to the respiratory function. Each of these papillæ contains a central canal, which is sometimes a mere dilated tube, but which in most species is more or less deeply sacculated; and the inner surface of these simple or complex cæca is lined with hepatic cells of irregular form.

406. In the greater number of *Mollusca*, however, as well as in most *Myriapoda*, *Insecta*, *Crustacea*, and *Arachnida*, we find the biliary organs considerably more detached from the digestive apparatus; having the form either of prolonged tubes, or of clusters of shorter follicles, which coalesce with each other in such a manner, as to discharge their contents into the alimentary canal by a small number of orifices; and being only connected with the alimentary canal, by the ducts through which their secretion is conveyed. The most simple type of this kind of structure is that which is met-with in *Insects;* in which class the biliary organs are usually regarded as consisting of a number of distinct filiform tubes (Fig. 57, *f*, *f*), lying in close apposition with the sides of the alimentary canal, but quite disconnected from it, except at the points where they enter it. Where their number is small, they are usually greatly elongated, being sometimes three or four times the length of the alimentary canal, and are tortuous and convoluted; and they usually open separately into the intestinal tube. But when numerous, they are proportionally short; and two or three of them frequently coalesce to form a common trunk, before entering the intestine. Their number varies considerably; in some *Coleoptera*, there are but two; in *Diptera*, there are generally four; in *Lepidoptera*, six; whilst in other orders, there are many more. In many larvæ, the biliary tubes are themselves furnished with lateral cæca; but these almost always disappear as the insect approaches the imago state; a less active biliary secretion being then apparently suffi-

cient. In the *Melolontha* (Cockchaffer), however, which has but two biliary vessels, these are of great length, and retain their lateral cæca. When carefully examined, these tubes are found to consist of a delicate tube of transparent membrane, the inner surface of which is covered with secreting cells; owing to the thinness of the tube, the cells often project, so as to give it a granulated appearance when viewed with the naked eye; and generally at a distance from their outlets, the sides of the tubes are so irregular, that they appear as if folded upon the secreting cells to keep them together (Fig. 174).* From the difference in size and degree of development between the cells of each tubulus, it seems probable that they originate at its upper extremity, that they are gradually being pushed-on towards its outlet by the growth of new broods behind them; and that, as they thus advance, they acquire an increase in size by their own inherent powers of development, at the same time drawing into themselves the peculiar matters which they are destined to eliminate from the circulating fluids. The cells, having attained their full growth, and completed their term of life, give-up their contents by the rupture or deliquescence of their walls; and these pass down the central cavity of the tube, to be discharged into the alimentary canal.—It is by no means certain, however, that this constitutes the whole of the biliary apparatus of Insects. The hepatic tubuli, when traced as far as possible from their intestinal connections, do not seem to terminate in free cæcal extremities, but lose themselves in a mass which has been usually regarded as simply adipose, but which has been shown by Dr. T. Williams† and Dr. C. H. Jones‡ to be composed of cells in various stages of development, closely resembling those found within the hepatic tubuli; these cells being usually inclosed in vesicles, which are sometimes free, but are sometimes connected with a network of tubuli. This has been termed by Dr. C. H. Jones the *parenchymatous* portion of the liver; and we shall hereafter see that it appears to combine the functions of the Liver with those of the Adipose tissue of higher animals (§ 417).

FIG. 174.



Structure of the biliary tubuli of *Musca carnaria* (flesh-fly):—A, portion of trunk and two branches, viewed by reflected light, and under a low magnifying power:—B, portion of a biliary tube more highly magnified, exhibiting the arrangement of the secreting cells, and the mode of distribution of the tracheæ.

407. The biliary apparatus of the *Myriapoda* closely resembles that of

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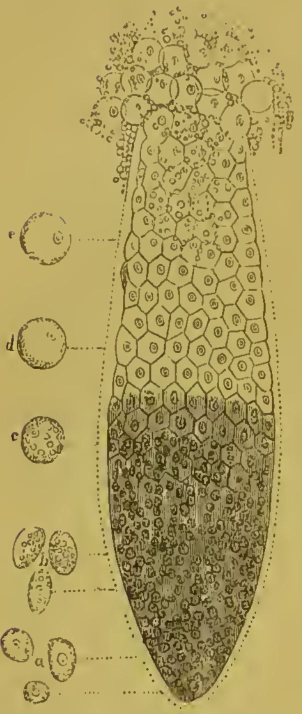
* See Leidy on the 'Comparative Structure of the Liver,' in "Amer. Journ. of Med. Sci.," Jan., 1848.

† See his Essay on the 'Comparative Anatomy of the Organs of Secretion,' in "Guy's Hospital Reports," 2nd Ser., Vol. iv.; from which many of the facts stated in this outline have been drawn.

‡ "Philos. Transact.," 1849, pp. 113, 114.

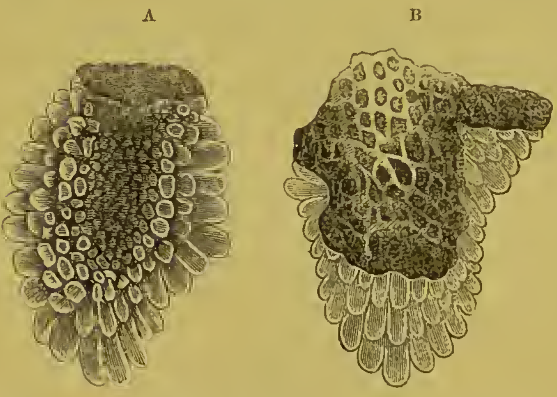
Insects; but in that of the *Crustacea* we have a much closer approximation to the Molluscan type, in which the biliary cells are inclosed within a multitude of follicles with distinct cæcal terminations (Fig. 175), aggregated together into a lobulated glandular mass. On a careful examination of these follicles, and a comparison of the size and contents of the cells at the bottom and towards the outlet, it becomes evident that they originate in the former situation, and gradually increase in size as they advance towards the latter. It is also to be observed, that the cells which lie deepest in the cæcum (*a, b*) contain for the most part the yellow granular matter, which may be regarded as the proper biliary secretion: but as they increase in size, they also increase in the quantity of oil-globules which they contain (*c*), until beyond the middle of the follicle, where they are found full of oil, so as to have the appearance of ordinary fat-cells (*d, e*). From this circumstance it happens, that when a cæcum is examined with the microscope, its lower half appears filled with a finely-granular matter, intermingled with nucleated particles; and the upper half with a mass of fat-cells, whose nuclei are obscured by the oily particles.* These follicles are clustered into lobules (Fig. 176), and discharge the products of their secreting action into a cavity in the centre of each; and from these it is collected by ducts that coalesce with each other to form a small number on either side, by which the product of the whole mass (Fig. 58, *e*) is discharged into the alimentary canal. Here, as in other Articulata, the hepatic organs present a perfect bi-lateral symmetry. In some of the Entomostracous Crustacea, however, as the common *Daphnia pulex*, the biliary apparatus is reduced to that simple condition, which it has been already described as presenting in the Bryozoa and lower Annelida; namely, a set of cells lodged in the walls of the intestine itself.—The structure of the biliary organs of the

Fig. 175.



One of the Hepatic cæca of *Astacus affinis* (Cray fish), highly magnified, showing the progress of development of the secreting cells, from the blind extremity to the mouth of the follicle; specimens of these, in their successive stages, are shown separately at *a, b, c, d, e.*

Fig. 176.



Lobule of Liver of *Squilla Mantis*; A, exterior; B, cut open.

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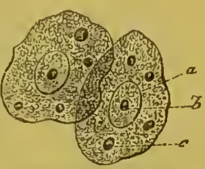
* Leidy, loc. cit.

Arachnida has not been fully made-out; but they would seem to partake rather of the character of those of the Crustacea, than of those of Insects. From the short, straight, alimentary canal, there pass-off on either side, in the abdominal region of the *Araneidæ*, but in the thoracic region of the *Scorpionidæ*, several pairs of cæca (Fig. 106, *e*), which subdivide and then lose themselves in a fatty mass of considerable size; this fatty mass has been usually regarded as nothing else than adipose tissue, but its hepatic character appears from recent observations to be unquestionable; and this circumstance adds weight to the opinion of those, who consider the great adipose mass in the body of Insects as biliary in its nature.

408. Throughout the *Molluscous* series, with the exceptions already named, the liver presents the same type of structure as in the Crustacea; and the chief advance which we see in ascending the series, consists in the increasing compactness of the glandular mass, and in its isolation from the walls of the digestive canal. For whilst, in the higher *Tunicata* and *Conchifera*, its lobules cluster round the pyloric portion of the stomach and the commencement of the intestine, and discharge their secretion by a multitude of separate orifices, these cluster in the higher *Gasteropoda* around the branches of a single or multiple common duct (Fig. 50, *l, l, l*), very much as in the Crustacea; and in *Cephalopoda*, the lobules are so connected together as to form a compact mass, nearly resembling the liver of Fishes, and (like it) removed to a distance from the intestinal canal, into which it pours its secretion by a single long duct.

409. In the *Vertebrated* classes, on the other hand, the plan of structure of the Liver undergoes a most marked change.* It no longer consists of a set of tubes or follicles, *containing* cells which stand to them in the relation of an epithelium; but it is mainly composed of a solid parenchyma, made-up of lobules or *acini*, each of which is composed of an aggregation of cells, *surrounded by* the ultimate ramifications of the biliary ducts. The *hepatic cells*, in the liver of man and of higher Vertebrata, are of a flattened spheroidal form (Fig. 177), their diameter being usually from 1-1500th to 1-2000th of an inch; each of them has usually a very distinct nucleus, the cavity surrounding which is occupied by yellowish amorphous matter, usually having one or two large adipose globules, or five or six small ones, intermingled with it; and the cell-wall is much more distinct than that of most other glandular cells, apparently denoting, therefore, an unusual degree of permanence in its character. These cells are very often arranged with their flattened sides in apposition with each other, in tolerably regular rows, radiating from the centres of the lobules towards their periphery; but this disposition is frequently exchanged for a plexiform or quite irregular one. They are imbedded in a diffused granulous plasma, in which young cells are observable; these being apparently formed by a collection of granular matter around free nuclei. It has been usually supposed that the hepatic cells ordinarily contain

Fig. 177.



Glandular cells of *Liver:—a*, nucleus; *b*, nucleolus; *c*, adipose particles.

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* It is interesting to remark, however, that, in the *Amphioxus*, the Liver is nothing more than a cæcal prolongation from the alimentary canal (Fig. 127, *l, l*) surrounded by hepatic cells, which are found also in the wall of the intestine itself.

biliary matter; but such, from the recent inquiries of Dr. Handfield Jones,* appears not to be the case, save in exceptional instances. But the peculiar *sugar* which is found in the blood of the hepatic vein (§ 362), is nearly always detectable in the cellular parenchyma: and the cells are sometimes found to be loaded with fat, those near the margins of the lobules being especially prone to this kind of accumulation. In Fishes and Reptiles, indeed, the hepatic cells generally are as full of oil as are those of the Crustacea; so that the livers of the Cod and other large fishes yield a considerable supply of it. In Birds, on the other hand, the hepatic cells are more free from fat-globules, than are those of Mammalia. These differences will be seen to have an important signification, when taken in connection with the probable action of the organ in these different groups (§ 417). The amounts of Sugar and of Fat in the hepatic parenchyma, are commonly in an inverse ratio the one to the other; and this is true also of the proportions of these substances in the blood of the hepatic vein.

410. The smallest branches of *Hepatic Ducts* are distributed through the fissures between the lobules; coming into relation, therefore, with their peripheries, but not being in peculiarly intimate contact with their parenchymatous tissue. If any branches come-off from the interlobular ducts, to enter the substance of the lobules, they are very few in number, and do not penetrate far. Their termination by closed extremities cannot be always distinctly seen; and sometimes they appear to "lose themselves," without any distinct endings; there is no sufficient ground, however, to believe that they ever form a plexus in the substance of the lobules, as some have maintained. The terminal portions of the ducts are crowded with nuclear particles and granular matter, resembling that which forms the intercellular plasma of the lobules; there are also cells which seem identical with those of the parenchyma, except that their walls seem thinner and their contents more pellucid; and fragments of similar cells are often to be seen; whilst the columnar epithelium which lines the larger ducts is almost or entirely wanting. These appearances, which correspond to those presented by the tubuli of the cortical substance of the kidneys, indicate that an active secretory function is going-on in this position; and point to the cells and nuclear particles within the biliary ducts, as the chief instruments in the elimination of bile.

411. With this change in the plan of structure of the Liver, a very marked change in the distribution of its Blood-vessels is connected. In the Invertebrata generally, this organ is supplied with blood from a single source; namely, by a branch of the principal systemic artery. This

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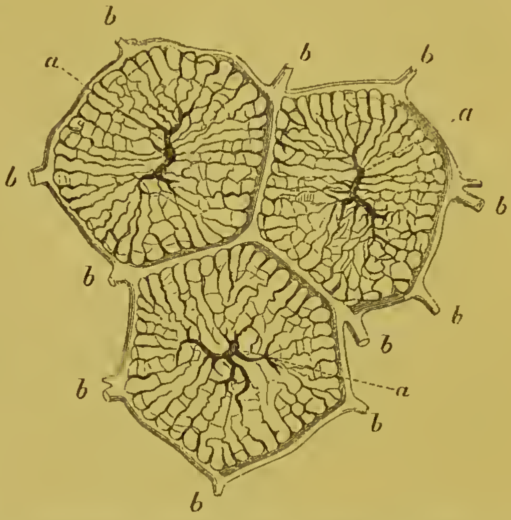
* The Author feels bound to state, that notwithstanding he had formerly accepted the statements of three eminent Anatomists, Prof. Retzius, Dr. Leidy, and Dr. Natalis Guillot, on the plexiform arrangement of the bile-ducts in the liver, as that which corresponded best with his own observations, and which was at the same time most probable in itself, he has been since convinced by the facts and arguments adduced by Dr. Handfield Jones, taken in connection with the parallel phenomena presented by the 'Vascular Glands,' that the view of the compound nature of the Hepatic structure which Dr. Jones was the first to propound, is really the correct one, and that the appearances which have led both himself and others to a belief in the plexiform arrangement of the bile-ducts, are fallacious. Dr. H. Jones's Memoirs 'On the Structure, Development, and Function of the Liver,' contained in the "Philosophical Transactions" for 1846, 1849, and 1853, are worthy of most attentive study.

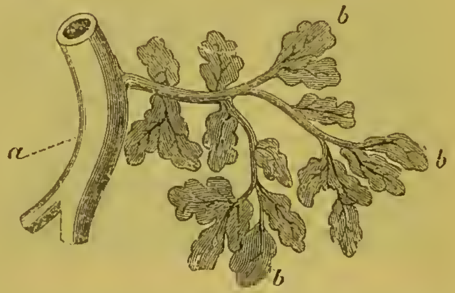
supply is still continued in the Vertebrated classes: for the *Hepatic artery*, given-off from the aorta, enters the liver with the biliary ducts, the ramifications of which it accompanies in their course to the individual lobules; and it is upon the walls of these ramifications, that its capillaries are chiefly distributed. But the principal supply of blood which the liver receives, is that brought to it by the *Portal* trunk, which is formed by the convergence of the veins of the digestive apparatus, with the addition, in the inferior Vertebrata of those of the posterior part of the body and tail (§§ 240, 245). The branches of this vessel (which, so far as regards its distribution, is as much an *artery* as is the aorta of Fishes) form a plexus between the lobules (Fig. 178); and from this plexus, a set of converging twigs proceeds towards the centre of each lobule, supplying a capillary network in its substance. In the centre of each lobule a radicle of the hepatic vein takes its origin, collecting the blood from the capillary network, and uniting with other radicles to form the trunk of the *Hepatic Vein*, by which the blood is carried into the Vena Cava. Owing to the peculiar position of the branches of the hepatic vein in the centre of each lobule, the lobules are appended (as it were) to these branches, like fruits upon a stalk (Fig. 179). The precise relation of the capillaries of the hepatic artery to those of the portal and venous systems, has not been ascertained beyond all doubt; but there seems reason to believe, with Mr. Kiernan, that the arterial capillaries discharge themselves into the ultimate ramifications of the portal vein; and that thus the blood of the former, having become venous by passing through them, mingles with the other venous blood conveyed by the portal trunk into *its* capillary network.—Now when we compare this very remarkable arrangement of the blood-vessels, with the arrangement of the parenchymatous tissue and the bile-ducts; when we call to mind, also, the typical structure of the 'Vascular Glands' (§ 370), with respect to whose *assimilating* action there can be no longer any reasonable doubt;

Fig. 178.



Horizontal section of three superficial lobules of the *Liver*, showing the two principal systems of blood-vessels; *a, a, intra*-lobular veins, proceeding from the Hepatic veins; *b, b, inter*-lobular plexus, formed by branches of the Portal veins.

Fig. 179.

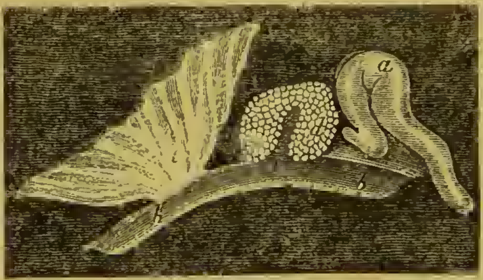


Connection of the *Lobules of the Liver* with the Hepatic Vein;—*a*, trunk of the vein; *b, b*, lobules depending from its branches, like leaves on a tree; the centre of each being occupied by a venous twig, the Intralobular Vein.

and when we recollect that there is ample evidence of a similar action being performed by the Liver (§ 366); it seems almost impossible to resist the inference, that the peculiar arrangement, both of the structural elements of the organ, and of the blood-vessels which supply it, has reference to this combination of *Assimilating* and *Secreting* operations: the *parenchymatous substance* of the liver, which is supplied by the portal system of vessels, being essentially the instrument of the former, whilst the *biliary ducts with their contained cells*, which are supplied by the hepatic artery, are (as in secreting glands generally) the organs whereby the latter are immediately effected. There seems no adequate reason, however, for asserting that the parenchymatous portion of the liver takes no concern in the secretion of bile; on the contrary, there seems every probability, from the intimate association of the two sets of actions—the converting and the secreting—in the same organ, that the latter is to a certain extent the *complement* of the former, biliary matters being eliminated in the very act of the metamorphosis to which certain of the components of the blood are subjected. The ordinary absence of biliary matter from the contents of the hepatic cells, is no objection to this view; since, if this matter be transmitted from cell to cell, towards the periphery of each lobule, as fast as it is formed, we should no more expect to find it in the parenchyma, than we expect to find any quantity of urea in the blood, when the kidneys are duly performing their functions. On the other hand, the fact that the hepatic cells are occasionally found to be turgid with biliary matter, when the final eliminating process is in some way interfered-with, seems to indicate that they *are* concerned in its separation from the blood; although this action may be altogether subordinate to the converting influence which they exercise upon the blood itself.*

412. The history of the *development* of the Liver in the higher animals, presents many points of most interesting analogy to the permanent conditions which the organ has been thus shown to possess in the lower; and at the same time throws light upon its function. The first rudiment of the gland is formed by a collection of cells (forming a portion of the original embryonic mass, that has not yet undergone conversion), in the neighbourhood of that spot in the intestinal canal, at which the hepatic duct is subsequently to discharge itself. This thickening increases, so as to form a projection upon the exterior of the canal; and soon afterwards the lining membrane of the intestine dips-down into it, so that a kind of cæcum is formed, surrounded by a mass of cells,

Fig. 180.



Origin of the *Liver* on the intestinal wall in the embryo of the Fowl, on the fourth day of incubation:—*a*, heart; *b*, intestine; *c*, everted portion becoming connected with liver; *d*, liver; *e*, portion of yolk-bag.

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* That the supply of blood brought by the Hepatic Artery is subservient in Vertebrata, as in Invertebrata, to the secretion of bile, is proved by the fact, that if the Vena Portæ be tied, the bile is still formed; whilst that it is *not the sole* source of the secretion, is indicated by the fact, that the amount of bile is diminished by the operation.

as shown in Fig. 180. Now here we have the obvious representation of the hepatic organs of the lower Invertebrata; which, in their simplest forms, are nothing else than isolated cells, situated in the walls of the alimentary canal itself; whilst, in their next grade, they are clustered round a cæcal diverticulum from its cavity. The condition of the Liver in *Amphioxus* is almost precisely represented by that of the embryo Fowl at the fourth or fifth day. The increase of the organ seems to take place by a continual new budding-forth of cells from its peripheral portion; and a considerable mass is thus formed, before the cæcum in its interior undergoes any extension by ramifications into it. Gradually, however, the cells of the exterior become metamorphosed into fibrous tissue for the investment of the organ; those of the interior break-down into ducts, which are at first developed independently, but subsequently come into continuity with the intestinal cæcum, and which are lined by muscular and fibrous tissues developed from the primitive cellular blastema; whilst those which occupy the intervening space, and which form the bulk of the gland, give origin to the cells of the parenchyma. As this is going on, the hepatic mass is gradually removed to a distance from the wall of the alimentary canal; and the cæcum is narrowed and lengthened, so as to become a mere connecting pedicle, forming, in fact, the main trunk of the hepatic duct.—Thus, then, the Liver of Vertebrata exists in the first instance, as a parenchymatous mass, which originates independently of any offset from the alimentary canal, and which essentially resembles that of which the Assimilating Glands are composed; and the history of its development, therefore, fully sanctions the view of the essentially double nature of the organ, which has been founded upon its structure and upon what can be ascertained of its *modus operandi.*

413. We have now to inquire into the characters of the *Bile*, and the purposes to which it ministers in the Animal economy.—Of the solid matter, which forms nearly a tenth part of the whole secretion, about an eighth part is composed of alkaline and earthy salts, corresponding with those found in the blood, but not bearing the same proportions to each other; soda being present (apparently in a state of actual combination with biliary matter) in such amount as to be peculiarly characteristic of this product. The organic constituents, which make-up the remainder of the solid matter of the bile, are acted-upon by reagents with peculiar facility, and are thus liable to be changed by the processes which are merely intended to separate them; and hence the accounts of them given by different Chemists have been far from being conformable with each other. It appears, however, that the fundamental component of Bile is a fatty or rather a resinous acid, now termed *Cholic*, from which nitrogen is altogether absent, whilst oxygen is present in it in only a small proportion, its formula being 48 Carbon, 39 Hydrogen, 9 Oxygen. This forms a 'conjugated' compound with *Glycine* (or gelatine-sugar), which is termed *glycocholic* acid; and it is this acid (formerly known as the *bilic* or *cholic* acid) which is the principal organic constituent of the bile of most animals; being united in that fluid with potash and soda as bases, and not having a sufficiently strong acidity to prevent its salts from possessing an alkaline reaction. The formula of this acid is $C_{52}\ H_{42}\ N\ O_{11} + HO$. —Cholic acid, however, forms another 'conjugated' compound with *taurine*, a neutral substance containing 25 per cent. of sulphur; and this

taurocholic acid, though existing in bile in smaller quantity than the preceding, has yet the important function of keeping it in solution, by its remarkable power of dissolving fatty bodies, and by its own ready solubility in water. Its formula is $C_{52} H_{45} NS_2 O_{14}$. A small quantity of *Cholesterine*, a white crystallizable fatty substance whose formula is $C_{36} H_{32} O$, also exists in bile; in many disordered states, this accumulates in large amount; and it forms the principal ingredient of most biliary concretions, being sometimes their sole constituent.—The peculiar Colouring matter of bile, or *Bile-Pigment*, is a substance which it is very difficult to examine satisfactorily, on account of its extreme instability. It is remarkable for the large proportion of carbon which it contains, this being no less than 68 per cent.; and it forms insoluble compounds with lime, which enter largely into the composition of some biliary calculi. Although its chemical characters have not yet been satisfactorily made-out, there seems much probability that it is related to the colouring-matter of the blood; for the addition of a mineral acid to the colouring-matter of bile produces remarkable changes in its hue, converting the yellowish matter successively into green, blue, violet, red, and brown; in fact, precisely into those colours which are exhibited by the colouring-matter of the blood, as left in an 'ecchymosis' in process of departure.

414. There is every probability that these substances exist in the blood, in a condition not very dissimilar to that in which they are found in the product secreted from it. Thus Cholesterine may be obtained from blood-serum, by an analytical process of no great complexity; and its presence there is manifested by its occasional deposit, as a result of diseased action, in other parts of the body, especially in the fluids of local dropsies. The Colouring-matter appears to be derived, directly or indirectly, from the hæmatine of the blood. Of the Biliary acids, however, it can only be said that their indefinite reactions have hitherto prevented their detection in the blood by chemical tests; and much yet remains to be learned regarding their history. From the considerations to be presently adduced, it would seem probable that biliary matter does not exist *as such* in the blood, previously to the formation of the secretion; but that its elements, derived from the disintegration of the tissues, are present in the circulating fluid under some more pernicious form, and are transformed by the agency of the liver, in order that they may be re-absorbed in a less noxious condition, to be finally eliminated by the respiratory process. It is certain that the effects of the *re-absorption* of bile into the blood, as seen in ordinary cases of jaundice dependent upon obstruction of the biliary ducts, are not nearly so injurious as are those of the *retention* of the elements of the secretion, consequent upon deficiency of the secreting power of the liver; for whilst, in the latter case, death speedily supervenes, if no other outlet be found for the excrementitious matter, no severe injury necessarily arises from the accumulation of biliary matter, in the former, to even such an extent that the tissues in general are tinged by it. And, as will presently appear, there is strong reason to believe that the re-absorption of biliary matter into the circulating current, is the means by which it is finally carried out of the system.

415. The special purposes answered by the secretion of Bile are still involved in considerable obscurity; but more definite and probably more correct ideas in regard to them are gradually being evolved; and the fol-

lowing may, perhaps be regarded as tolerably well-established truths.—In the first place, the bile must be considered as an *excrementitious* substance, derived from the disintegration of the tissues, or from the decomposition of the elements of the blood; and it serves especially to remove from the blood the *hydro-carbonaceous* portion of the effete matters, the *nitrogenous* being eliminated in the urine. It has been pointed-out by Prof. Liebig, that if we add to half the formula representing the ultimate composition of *bile*, the formula of *urate of ammonia* (which is the characteristic component of the urine of all animals save Mammalia), the sum gives the proportionals of the ultimate components of dried *blood* or of *flesh*, with the addition of 1 eq. of oxygen and 1 eq. of water. For;—

Half an equivalent of Biliary matter . .	=	38 C,	33 H,	N,	11 O
One equivalent of Urate of Ammonia . .	=	10 C,	7 H,	5 N,	6 O
The sum of which . .	=	48 C,	40 H,	6 N,	17 O

And, in like manner;—

Formula of Blood	=	48 C,	39 H,	6 N,	15 O
1 Eq. of Water + 1 Eq. of Oxygen . . .	=		H		2 O
		48 C,	40 H,	6 N,	17 O

Now although it must be admitted that, by a dexterous management of formulæ, almost any kind of transformation may be effected *on paper*, yet this coincidence, without any management at all, is so close, that it cannot be regarded as accidental; and we seem fairly entitled to look upon the principal materials of the animal fabric as partly resolving themselves in their disintegration, into the characteristic components of the two principal excretions, the Urinary and the Biliary. Of course this resolution only expresses *a part* of the metamorphoses which the tissues undergo; for the creatine and creatinine of the urine, and the fæcal matters of the alimentary canal, must be regarded in the same light; and there are doubtless other excrementitious matters (included in the general term 'extractive'), of which we know still less, that must be attributed to a like origin. But it seems satisfactorily to account for the components of the biliary matter; since they form the *complement* of the urinary; so that the formation of each excretion seems to involve that of the other.—Now, that the Bile is in its essence an excrementitious product, and that the assistance it may afford in the digestive process is *not* the principal purpose of its secretion, appears further from this; that it is eliminated during the latter part of embryonic life, and that it then accumulates in the alimentary canal, forming a large part of the meconium which is discharged soon after birth. But from the time that respiration commences, and during the whole subsequent life, it appears from chemical analysis of the fæces, that not much of the bile, save its colouring matter, is evacuated in the state of health; *so that a large part of that which is poured into the alimentary canal, must be re-absorbed through the blood-vessels and lymphatics of its walls.* And there can be little doubt that, when thus re-absorbed, and taken into the current of the circulation in a less noxious form than that in which its elements previously existed, the biliary matter is chiefly eliminated by the respiratory process; its sulphur, however, being oxidised, that it may be carried-off by the urine, and its soda being eliminated by the same channel. In this point of view, the secretion of bile may be regarded as the intermediate stage between the disintegration or 'waste' of the tissues, and the final elimination of the combustible products of that waste by the instrumentality of the lungs.

416. But that the Bile performs some subsidiary function in the Digestive process, would also seem beyond doubt. It is not, however, a sufficient indication of this, that we should find the outlet of the hepatic organs, through the entire Animal Kingdom, to be in the part where digestion is most actively going-on; for it might be, that the discharge of the bile into the upper part of the alimentary canal, has reference merely to its re-absorption. But it appears from the results of numerous experiments, that when the bile-duct is divided, and its extremity is drawn out of the body, in such a manner that it can freely discharge the hepatic secretion, but this is prevented from passing into the alimentary canal, the animals, although they do not at first appear to suffer much in health, gradually become emaciated, and at last die of inanition, unless they are allowed to receive-back the bile by licking the wound, in which case they survive. And it seems proved by the investigations of Lehmann and Frerichs, that although the pancreatic fluid certainly possesses considerable power of 'emulsifying' the oleaginous matters in the alimentary canal, yet that it answers this purpose much more effectually when mingled with bile, which possesses an emulsifying power of its own.

417. Thus, then, if we bring together all the facts at present in our possession, with reference to the offices of the Hepatic apparatus, they seem to lead to these conclusions.—1. That it is essentially an organ of excretion, designed to remove from the circulating fluid that portion of the products of disintegration, of which the principal component of the urinary excretion is the 'complement.'—2. That in doing this, it converts the greater part of the excrementitious matters into the conjugated biliary acids; substances which can be reabsorbed with less injury, and which, after performing their part in the digestive process, are taken-back into the blood, to be eliminated by oxidation through the lungs.*—3. That the temporary presence of bile in the alimentary canal is subservient to the digestion and absorption of the non-azotized compounds, and in some degree to that of the albuminous also.—4. That in Vertebrated animals, it is also an *assimilating* organ, exerting its agency upon the alimentary materials brought by the blood (§ 366), converting the crude albuminous matters into blood-albumen, and preparing, both from the substances newly introduced, and from those which (having served their purpose in the body) have become effete, peculiar saccharine and oleaginous compounds, which supply the *pabulum* for the respiratory process.—Since we are thus to regard the production and separation of Fatty matter as one of the great purposes answered by the Liver, it need not surprise us to find that this organ should frequently serve, not only to prepare this, but also to store it up; and such we might expect to be the fact especially in those classes of animals, in which its final elimination by the respiratory

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* When an unusually large quantity of bile is poured into the intestinal canal, as after the action of a mercurial purgative, or in 'bilious diarrhœa,' the greater portion of it escapes reabsorption, and is ejected *per anum*.

action is slow. Now we have found that the great bulk of the liver in the Crustacea, Mollusca, and cold-blooded Vertebrata, has reference apparently, not to a large production of bile, but to an accumulation of fat: whilst in Mammalia the fat is in very small amount, unless the respiration be impeded; and in Birds, whose respiration is pre-eminently active, scarcely any traces of fat are to be found. The fat thus stored-up in the liver will probably be taken into the current of the circulation, as it is wanted, by the blood which passes through the organ; and may never be discharged as an excretion into the alimentary canal.*

418. *Of the Kidneys and the Urinary Excretion.*—The Kidneys are to be regarded as purely *excreting* organs; their sole function being to separate from the blood certain matters which would be injurious to it if retained; and these matters being destined to immediate and complete removal from the system. These glands almost always present a tubular structure; the required extent of surface being given, not by the multiplication of separate follicles, but by a great prolongation of the individual cæca. The urinary organs do not acquire any great development among the Invertebrata generally, and all traces of them are frequently wanting. In *Insects* and *Arachnida* they present themselves as a group of cæcal tubuli, discharging themselves into the cloacal termination of the alimentary canal (Fig. 106, *h, h*); and similar tubuli are found in some of the higher Crustacea.—In the Molluscous series, however, the urinary organs, where they exist, possess rather a follicular character. A glandular mass is found in some *Conchifera*, consisting of an elongated sacculus that lies on each side of the dorsal margin between the pericardium and the adductor muscle, and opening by a minute orifice into the cavity of the mantle; and this, though formerly regarded as a calcifying gland, seems to be really a kidney; for the parenchyma of its walls readily decomposes into minute corpuscles, which consist chiefly of uric acid, and which are probably to be regarded as having been originally secreting cells, that have become filled with that excretory product. A similar organ, composed of a series of lamellæ enclosed in a sac that is continued into an excretory duct opening externally near the anus, is found in many Gasteropods; and the lamellæ are covered with closely-set thin-walled cells, which, besides a transparent liquid, contain a brownish nucleus that is composed of uric acid. It is remarkable that in animals so highly organised as the *Cephalopoda*, the presence of a proper renal organ should have been so long undetermined. The surmise of Prof. Mayer, that the masses of follicles connected with the great veins (Fig. 125, *r*) are to be regarded as a urinary apparatus, has been confirmed by Siebold, who states that they contain uric acid.

419. When we pass to the Vertebrated series, however, we usually find the Urinary organs attaining a large size in the class of *Fishes;* but their type of conformation is low. They very commonly extend through the whole length of the abdomen; and consist of tufts of uniform-sized

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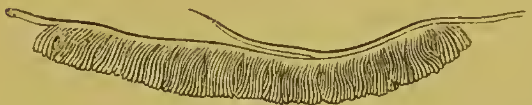
* The doctrine that the agency of the Liver is preparatory to the Respiratory function, was first propounded by Prof. Liebig ("Animal Chemistry," 1842); and although it has had to contend against many important objections, it has gradually made its way into Physiological Science:—in the form in which it is above stated, the author believes that it will be found consistent with all the facts at present known.

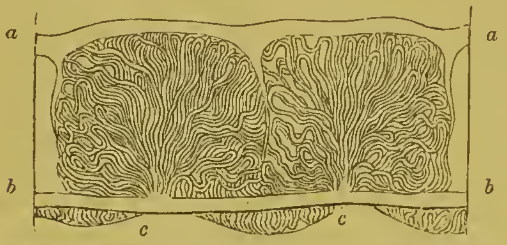
tubules, which shoot forth transversely at intervals from the long ureter, and are connected together by a loose web of areolar tissue, that supports the network of vessels distributed upon their walls. This condition of the urinary apparatus is very analogous to that of the Corpora Wolffiana, or temporary renal organs of the embryo of the higher Vertebrata, which are afterwards superseded by the permanent kidneys (§ 422). In the lowest members of the class, however, the structure is yet simpler; for in the *Cyclostomi*, each long duct sends-off at intervals, instead of a bundle of tubuli, a short wide tube which communicates with a single cæcum; and at the bottom of this is a small 'vaso-ganglion,' or convoluted plexus of blood-vessels, which reminds us of the Corpora Malpighiana in the kidneys of higher Vertebrata. In the *Amphioxus*, the only rudiment of a kidney is the slightly-opaque, slender, elongated glandular-looking body (Fig. 127, *h*), which is considered by Prof. Owen to possess this character, though its structure has not yet been fully elucidated.

Fig. 181.



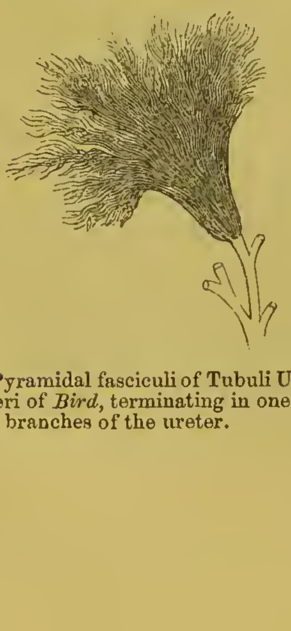
Kidney of fœtal *Boa:*—the urinary tubes as yet short and straight.

Fig. 182.



Portion of Kidney from *Coluber:—a, a,* vascular trunk; *b, b* ,ureter; *c, c,* converging fasciculi of tubuli uriniferi.

Fig. 183.

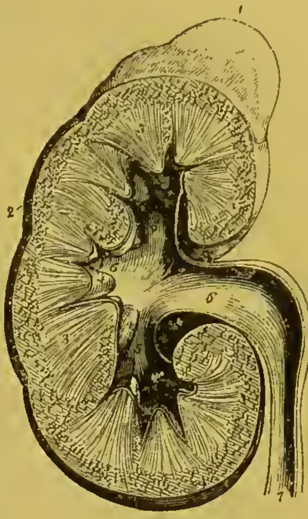


Pyramidal fasciculi of Tubuli Uriniferi of *Bird*, terminating in one of the branches of the ureter.

420. The size of the Kidneys is usually considerable in *Reptiles;* but their form differs greatly in the several orders of the class, being narrow and much elongated in Batrachia and Ophidia, but broader and shorter in Sauria and Chelonia. Their essential structure, however, is nearly the same throughout; for the ureter gives off a large number of transverse cæca, which are short and nearly straight in the lower Reptiles and in the early condition of the higher (Fig. 181), but which in the more developed conditions of the organ become long and convoluted (Fig. 182), each group forming a lobule, which receives branches from the portal trunk that supplies the organ with blood. In the Crocodile, the distinction between the *cortical* and the *medullary* portion of the kidney becomes evident; the former being the part in which the blood-vessels are most copiously distributed, and in which the tubuli have the most convoluted arrangement; whilst the tubuli in the latter are straighter, and converge more directly to the points at which they discharge themselves into the ureter. The *Corpora Malpighiana* (§ 421), where they exist in this class, are scattered through the entire substance of the kidney; not being restricted, as in the higher animals, to its cortical portion.—In *Birds*, too, the kidneys are of large size; and they present also a greater compactness of texture. The lobules of which they are composed, can often

not be distinguished externally; but they are connected with separate branches of the ureter, and each consists of a converging bundle of tubuli uriniferi, forming its 'medullary' portion (Fig. 183), and of the dichotomous ramifications of these in the outer part of the lobule, of which they constitute the 'cortical' portion.—It is in *Mammalia*, however, as in Man, that the organ becomes most compact, and the distinction between its cortical and medullary portions most clearly marked. The separate clusters of tubes do not now open into distinct branches of the ureter; but discharge their contents into a capacious cavity formed by the dilatation of the ureter in the interior of the kidney (Fig. 184), which looks (in section) as if it were doubled-together around it. The lobules composed of these separate clusters are usually blended together so closely, that they can neither be distinguished externally, nor be separated from each other anatomically; in many of the lower Mammalia, however, the lobulated character which this gland always possesses at an early stage of its development (§ 422), is permanently retained.

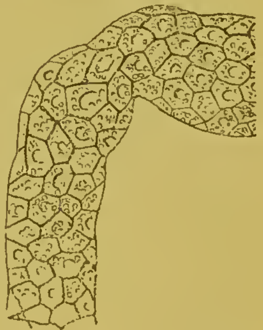
Fig. 184.



A section of the *Human Kidney*, surmounted by the Supra-Renal capsule; the swellings upon the surface mark the original constitution of the organ, as made-up of distinct lobes:—1. The supra-renal capsule. 2. Cortical portion of the kidney. 3, 3. Its medullary portion, consisting of cones. 4, 4. Two of the papillæ projecting into their corresponding calices. 5, 5, 5. The three infundibula; the middle 5 is situated in the mouth of a calyx. 6. The pelvis. 7. The ureter.

421. The proper secreting apparatus consists of the epithelial cells of the tubuli uriniferi of the cortical substance, which draw the peculiar elements of the urinary excretion from the vascular plexus which surrounds them, and then deliver these up, to be carried-off through the tubuli of the medullary portion, to their terminations in the ureter. The epithelium of the convoluted or secreting portion of the tubuli, is of the kind that is termed 'spheroidal' or 'glandular,' its cells having a more or less rounded form, and adhering loosely to the basement-membrane on which they lie; they are granular and opaque, apparently containing a considerable quantity of solid matter; whilst their walls are so delicate, that they frequently dissolve-away when water is added, so that the *débris* of the renal epithelium are not visible in healthy urine. On the other hand, the epithelium of the straight or medullary portion of the tubuli is of the 'tesselated' or 'pavement' kind; its cells are flattened and polygonal (Fig. 185), and are applied closely against the walls of the tubuli; their contents are more transparent, and their walls firmer; and it does not seem probable that they take any part in the elimination of the secretion. The Kidney contains another apparatus, of a very peculiar description, which appears specially destined for the separation of the superfluous *fluid* of the blood, by a process of simple transudation. When a

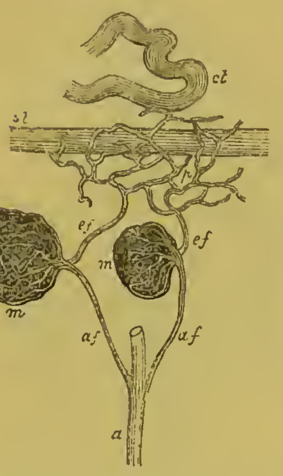
Fig. 185.



Portion of *Tubulus Uriniferus*, with its tesselated epithelium.

section of the cortical substance is slightly magnified, the cut surface is seen to be studded with a number of little dark points, each one of which, when examined under a higher magnifying power, is found to consist of a knot of minute blood-vessels, formed by the convolutions of thin-walled capillaries (Fig. 186, *m*). These bodies, termed *Corpora Malpighiana* after their first discoverer, are included in little flask-shaped capsules, the necks of which are continuous with the tubuli uriniferi, so that these may be considered as sending-off little diverticula to invest the Corpora Malpighiana, which lie freely within them.* Each of these little vascular knots is directly supplied by a branch of the renal artery (Fig. 186, *a*, *b*), which, when it reaches the capsule, subdivides into a group of capillaries; and these, after forming the convoluted tuft (*m*), coalesce into a single efferent trunk (*ef*). The efferent trunks of the several Malpighian bodies discharge their blood into the capillary plexus which surrounds the tubuli uriniferi; and it is from this that the solid matter of the urinary secretion is elaborated. Thus the whole Malpighian system of vessels may be considered (as Mr. Bowman has pointed-out) in the light of a *portal* system within the kidney; the efferent vessels of the Corpora Malpighiana being collectively the representatives of the Vena Portæ, since they convey the blood from the first (or systemic) to the second (or secreting) set of capillaries. In Reptiles (in which, as in Fishes, the Kidney is partly supplied from the hepatic portal system § 242), the efferent vessels of the Malpighian bodies, which receive their blood (as elsewhere) from the renal artery, unite with the branches of the Portal vein to form the secreting plexus around the tubuli uriniferi; so that this plexus, like the secreting plexus of the Liver (§ 411), has a double source, the vessels which supply it receiving their blood in part from the capillaries of the organ itself, and in part from those of other viscera. In Mammalia, however, the secreting plexus is entirely supplied by the efferent vessels of the Corpora Malpighiana; though in Birds the oviparous type of distribution seems still to prevail to a certain extent (§ 245).—The necks of the flask-shaped diverticula of the tubuli uriniferi, are easily seen, in the cold-blooded Vertebrata, to be lined with a *ciliated* epithelium; by the agency of which, the water filtered-off through the Malpighian capillaries is driven along the tube. No cilia have yet been detected in the tubuli of Birds or Mammals; but several considerations render their existence probable.

FIG. 186.



Distribution of the Renal vessels, from Kidney of *Horse*:—*a*, branch of Renal artery; *af*, afferent vessel; *m*, *m*, Malphigian tufts; *ef*, *ef*, efferent vessels; *p*, vascular plexus surrounding the tubes; *st*, straight tube; *ct*, convoluted tube.

422. In the embryological *development* of the Kidneys of the higher Vertebrated animals, we have a very interesting example of the evolu-

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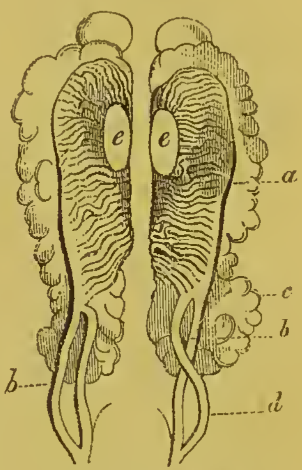
* By Mr. Bowman, the first discoverer of this curious relation, it was supposed that the flask-shaped dilatation was formed by the expansion of the *extremity* only of the tubulus uriniferus ("Philos. Transact." 1842): subsequent investigations have proved, however, that the Corpora Malpighiana are connected with the sides, as well as with the extremities of the tubuli, so that each tubulus is in relation with several of them.

tion of an organ, which is to serve only a temporary purpose in them, but which remains as the permanent instrument of the function in the lowest class, although superseded in the higher by an organ formed upon a more elaborate type. The first appearance of anything like a Urinary apparatus in the Chick, is seen on the second half of the third day; and the form then presented by it is that of a long canal, extending on each side of the spinal column, from the region of the heart towards the allantois; the sides of which present a series of elevations and depressions, indicative of the incipient development of cæca. On the 4th day, the *Corpora Wolffiana*, as they are then termed, may be distinctly recognized as composed of a series of cæcal appendages which are attached along the whole course of the first-mentioned canal, opening into its outer side (Fig. 187, *a*); and thus closely corresponding with the condition of the (so called) kidneys of Fishes (§ 419). On the 5th day, these appendages are convoluted, and the body which they form acquires increased breadth and thickness; they evidently then possess a secreting function, and the fluid which they separate is conveyed by the duct of each side (*b*, *b*) into the *allantois*, a sac which, though employed as a temporary respiratory organ (CHAP. XI.), is also used as a urinary bladder. Vestiges of Corpora Malpighiana may even be detected in connection with the secreting cæca. These bodies remain as the permanent urinary organs of Fishes; but in the higher Vertebrata they give place to the true kidneys, the development of which commences in the Chick at about the fifth day. They are seen on the sixth as lobulated greyish masses (*c*), which seem to sprout from the outer edges of the Wolffian bodies, but which are really independent formations, springing from a mass of blastema behind them; and as they gradually increase in size, and advance in development, the Wolffian bodies retrograde; so that at the end of fœtal life, the only vestige of them is to be found as a shrunk rudiment, situated (in the male) near the testes, which are originally developed (*e*, *e*) in contiguity with them.—The Kidneys, in the Human embryo, soon after their first development in the manner just described, consist of seven or eight lobes, the future 'pyramids;' their excretory ducts still terminate in the same canal as that which receives those of the Wolffian bodies and of the sexual organs; and this opens, with the rectum, into a cloaca, analogous to that which remains permanent in the Oviparous Vertebrata. The lobulated appearance of the kidney gradually disappears, partly in consequence of the condensation of the areolar tissue which connects the different parts, and partly through the development of additional tubuli in the interstices. Thus we have, in the development of the Urinary apparatus, the same kind of progress from the more general to the more special type, as we have seen in the Respiratory; and it is not a little curious that the more general form of both should be retained in the same class, namely that of Fishes. There is this difference, however, between the two cases; that whilst the

FIG. 187.



State of the *Urinary* and *Genital* apparatus in the early embryo of the Bird:—*a*, Corpora Wolffiana; *b*, their excretory ducts; *c*, kidney; *d*, ureter; *e*, *e*, testes.

branchial arches of higher animals are not ever developed so far as to be instrumental in the respiratory function, their Corpora Wolffiana appear to be true temporary kidneys, eliminating a real urinary product (§ 424).

423. The Urine of Man and of *Mammalia* generally, is characterised by the large proportion of *water* which it contains, in comparison with its solid constituents; the latter being seldom above 5 parts in 100, and being very commonly less. The two, in fact, bear no constant relation to each other; for the amount of liquid in the secretion depends mainly on the degree of fulness of the blood-vessels; while that of the solid matter is governed by that of the previous 'waste' of the tissues. It would seem as if a much larger quantity of water is habitually taken-in, than is needed in the system; in order to provide for the reduction of the temperature of the body by cutaneous Exhalation, when it might otherwise be unduly elevated (§ 332). But if the usual quantity of water be not thus drawn-off, in consequence of the depression of the external temperature, or the saturation of the atmosphere with dampness, or if an unduly large amount have been absorbed, the Kidneys afford the channel for its elimination. This appears to be the special function of the Malpighian bodies; whose thin-walled capillaries allow the transudation of water to take place under a certain pressure, into the tubuli uriniferi; and thus act the part of regulating valves, permitting the passage of whatever is superfluous, while they retain the liquid that is needed in the system. In *Birds,* on the other hand, it would seem as if there is much less occasion for any provision to reduce the temperature, which is habitually kept up at a standard higher than that of any other animals; and they accordingly drink very little, so that the proportion of water in their urine is only sufficient to give it a semi-fluid consistence. The urinary excretion of *Reptiles* appears to be in general yet more solid; for these animals usually ingest but little water, and a part of this is given-off by cutaneous exhalation when the external temperature is high. The condition of that of *Fishes* and *Invertebrata* appears to be generally the same; but from this statement the 'bombardier' beetles must be excepted, which emit their urine, as a means of defence, in little puffs of vapour, having a very acrid character, and believed to contain nitric acid.—The *solid matter* of the urine partly consists of Organic Compounds formed within the body, as the result of the disintegration of the tissues, or of the decomposition of substances taken-in as food; and partly of Inorganic Salts, such as normally exist in the serum of the blood, their proportion being liable to an increase, however, under circumstances to be presently alluded-to.

424. The Organic Compounds are not the same in all animals; but yet they are nearly related to each other, and agree in the very large proportion of nitrogen which they contain. The most characteristic of them, when completely isolated, present a *crystalline form,* which seems to be completely incompatible with the possession of plastic or organisable properties, and marks their affinity to inorganic substances. In the Urine of Man, the most characteristic ingredient is *Urea,* a neutral substance, isomeric with cyanate of ammonia, which is very soluble in water, and may be crystallised-out in transparent, colourless, four-sided prisms. When pure, it has very little tendency to decomposition; but when associated with other substances which act as 'ferments,' it takes to itself the oxygen and hydrogen of 2 equiv. of water, and resolves itself into

carbonate of ammonia; and as this change occurs in all urine after it has left the body (the mucus of the bladder serving as the 'ferment'), the carbonic acid and the ammonia which have been decomposed in the production of the organic compounds of Plants (§ 120), are restored to the Inorganic world.—The Urine of Man also contains a small quantity of *Uric Acid*, a substance which is not readily soluble in pure water, but which is more easily dissolved by water holding phosphate of soda in solution, especially when warm; and this seems to be its condition in human urine. It is also more readily dissolved when in combination with ammonia; and in this condition it forms a large part of the almost solid urine of Serpents, which also contains, however, like the urine of Birds, a large quantity of undissolved uric acid. When separated and purified, uric acid forms a glistening snow-white powder, apparently amorphous, but shown by the microscope to consist of minute but regular crystals. It is tasteless and inodorous; and its acid reaction is very feeble.—Uric Acid is replaced in the Urine of Herbivorous Mammals by *Hippuric Acid;* which is also normally present (though in small quantities) in the urine of Man, especially after the use of vegetable food. When pure, it crystallizes in long transparent four-sided prisms, and has a strong acid reaction, with a bitterish taste; it is much more soluble in cold water than uric acid, and it dissolves readily in warm. When dissolved in a liquid containing putrescent albuminous compounds, hippuric acid is converted into benzoic acid, ammonia being at the same time given-off.—In the fluid of the Allantois of the fœtal Calf (and probably also of other animals), which may be regarded as a temporary urinary bladder, receiving the product of the secreting action of the Corpora Wolffiana or temporary kidneys, is found another substance, termed *Allantoin*, which may be artificially obtained from uric acid by boiling it with peroxide of lead. This is a neutral substance, forming small but most brilliant prismatic crystals, which are destitute of taste, and moderately soluble in cold water; when decomposed by strong acids, it is resolved into ammonia, carbonic acid, and carbonic oxide; and when acted-on by alkalies, it is resolved into ammonia and oxalic acid.—Two other substances, *Creatine* and *Creatinine*, have recently been discovered in the urine of Man and the Mammalia, which seem intermediate in character between the albuminous compounds and the characteristic components of the urinary excretion. *Creatine*, which may be obtained from the juice of raw flesh, is a neutral substance, having the form of colourless, prismatic crystals, sparingly soluble in cold water, but dissolving readily in warm. By the action of strong acids, creatine is converted into *creatinine*, which only differs from it in composition by containing two proportionals less of the elements of water, but is a substance of very different chemical relations, having a strong alkaline reaction, and serving as a powerful organic base to acids. It pre-exists in the juice of flesh to a small extent; and is found, in conjunction with creatine, in the urine. When long boiled with caustic baryta, creatinine is gradually resolved into urea.—The composition of these substances in relation to each other, and to that of Albuminous compounds, is shown in the following table; which gives for each the number of combining equivalents of its individual components, and the per-centage proportion which the nitrogen bears to the whole.

		Carbon.	Hydrogen.	Nitrogen.	Oxygen.	Per Centage of Nitrogen.
Albumen	Liebig . .	49	36	6	14	15·67
	Mulder . .	40	31	5	12	
Urea		2	4	2	2	46·67
Uric Acid		5	2	2	3	33·33
Hippuric Acid (hydrated)		18	9	1	6	7·82
Allantoin (hydrated) . .		8	5	4	6	35·44
Creatine		8	9	3	4	32·06
Creatinine		8	7	3	2	37·17

Hence the proportion of Nitrogen in the components of Urine ranges from double to triple that which exists in the Albuminous constituents of the living fabric; the only exception being in the case of Hippuric acid,* whose proportion of nitrogen is only half of that which exists in albumen, whilst its per-centage of Carbon is triple that which is contained in Urea. —Besides the foregoing substances, the Urine contains others whose nature has not yet been clearly determined; these are at present included under the general designation *Extractive matters,* and appear to consist in part of non-azotised compounds in a state of change.—The Inorganic Compounds which are found in the urine, partly consist of salts which are taken-in as such in the food; and partly of salts which are formed in the economy, the acids being furnished by the oxygenation of bases contained in the aliment, and an ammoniacal base being supplied by the decomposition of the albuminous compounds. To the former class belongs *chloride of sodium* (common salt), of which the urine always contains a large amount, obviously derived directly from the serum of the blood; and also the *phosphates of lime and magnesia,* the proportion of which in the urine appears entirely to depend upon the amount ingested in the food. To the latter class belong the *alkaline sulphates and phosphates;* whose acids appear to be chiefly formed by the oxygenation of the sulphur and phosphorus which are constituents of all the albuminous compounds used as food; while their alkaline bases, when not ammoniacal, are supplied by the potass and soda that were ingested in combination with citric, tartaric, oxalic, and other organic acids, these acids being decomposed in the system, and carried-off by the respiratory process. Such weakly-combined bases abound in the food of Herbivorous animals, but they are for the most part wanting in that of the purely Carnivorous; and the fixed alkalies of their urine are replaced in greater proportion by ammonia.

425. Hence we may say, that the Urinary excretion is specially destined (1), for the elimination of those products of the disintegration of the tissues, and of the metamorphoses taking place in the living body, which are of a highly azotized nature, or which, being in the condition of soluble salts, readily find their way by transudation through membranous cell-walls that hold back the albuminous element of the serum

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* It has been surmised that, as Hippuric acid is usually restricted to the urine of animals of whose food non-azotized substances form a large part, it must have some other source than the metamorphosis of the organised tissues, and must be formed by the union of the products of this operation with some of the farinaceous or other superfluous components of the food; but there is adequate evidence that it may be formed by the metamorphosis of albuminous substances; and its presence may be accounted-for by any circumstance (whether deficient respiration, or an excess of hydro-carbonaceous matters in the food,) which tends to prevent the oxidation of the highly-carbonized products of the waste of the tissues. See the Author's "Human Physiology," 4th Ed., § 59.

of the blood (§ 421); it is also obvious (2) that the kidneys are destined to remove, in the same form, whatever components of the food are superfluous, and are undergoing decomposition from not being applied to the purposes of nutrition; and it is further their office (3) to draw-off any soluble saline matters taken into the system, which are either useless or injurious to it.—Although the relations of the amount of the organic compounds in the urine, to food, exercise, &c., have been as yet studied almost entirely in the Human subject, there can be no reasonable doubt that the same general rules will be found to hold good elsewhere. The proportion of *urea* which is voided in a given time is proportional, *cæteris paribus*, to the amount of *muscular exertion* that has been put forth; showing that its presence depends in part upon disintegration of the Muscular tissue. But this is not its sole source. For it is greatly augmented, also, by an excess of azotized compounds in the food; these compounds, as already shown (§ 390), not being applied to the nutrition of the muscular substance, unless a demand for augmented formation has been created by previous functional activity. Thus, the average proportion of Urea in the Human urine, under ordinary circumstances as to food and exercise, appears to be from about 20 to 35 parts in 1000; but it may be raised to 45 parts by violent exercise, and to 53 parts by an exclusively animal diet; whilst it may fall as low as to 15 or even 12 parts, when the diet is deficient in azotized matter. The average daily amount excreted by adult *males*, is about 430 grains; by adult *females*, about 300 grains; in *children* of eight years old, it is nearly *half* what it is in adults; whilst in *very old persons*, the quantity sinks to *one-third* or even less; showing that the proportion is greatly influenced by the rapidity of interstitial change at different periods of life (§ 392). There can be no doubt that *creatine* and *creatinine* have the same origin and character, since they are actually found in the juice of flesh, as well as in the urine.—So the proportion of the *alkaline phosphates* in the urine is found to bear such a close relation to the previous energy of the *nervous system*, that there can be little doubt that, *cœteris paribus*, their amount may be taken as a measure of its disintegration by functional activity. It has been pointed-out that, for the maintenance of this activity, a constant supply of arterialised blood is a necessary condition; and whilst the other elements of the nervous tissue (whose composition is almost entirely adipose) will be carried-off by oxygenation in the form of carbonic acid and water, the phosphorus which largely enters into it will be oxygenated, and taken back into the blood in the form of phosphoric acid, uniting there with alkaline bases, as already explained.—The proportion of *extractive matters* appears chiefly to depend upon the nature of the food; being greatly augmented by an exclusively vegetable regimen, and greatly diminished by an exclusively animal diet.—The importance of the urinary excretion in removing superfluous or injurious saline compounds from the system (the introduction of which into it has taken place by endosmotic action, § 169), is further shown by the increase in the secretion which most of these substances produce; this increase being the result of an augmented determination of blood to the kidneys, and a consequently increased transudation of its watery portion, carrying these substances with it. And further, it has been found, that poisonous substances (such as arsenious acid), whose rate of elimination through this channel is not in general sufficiently great to prevent them from exerting their injurious effects upon the system, may be carried out of the body with such rapidity as to render them innoxious, if diuretics (or medicines that augment the urinary secretion), be given at the same time.

426. *Cutaneous and Intestinal Excretions.*—The exhalation of superfluous water is by no means the only function performed by the Cutaneous glandulæ (§ 331). For the perspiratory fluid contains a considerable amount of solid matter, the proportion of which is sometimes as much as 12½ parts in 1000. The greatest part of this consists of animal matter, which is apparently an albuminous compound in a state of incipient decomposition, being not improbably composed in great part of the epithelium-cells cast-out from the tubes of the glandulæ; but in addition to this, urea has been recently detected in the perspiratory fluid, in no inconsiderable quantity; so that the Skin may be considered as supplementary to the kidney in its excretory action. Besides this animal matter, the perspiratory fluid also contains saline substances, which are for the most part those existing in the blood. The compounds of lactic and acetic acid, however, seem to be specially determined to this surface, and the perspiration thus occasionally possesses a very sour odour and an acid reaction.—Of the glandulæ of the mucous surface of the Alimentary canal, some effect the elimination of the gastric and other fluids concerned in the digestive process,* and secrete mucus for its protection; but there is strong evidence that the office of some of the glandular follicles, with which the lower part of the intestinal tube is thickly set, is to eliminate from the blood those *putrescent* matters, which would otherwise accumulate in it to its injury, whether as the results of the normal *waste* of the system, or as the products of the action of substances introduced into it, which operate as *ferments.* It has been already mentioned (§ 165), that the peculiar putrescent matter which is characteristic of the *fæces,* is not directly derived from the decomposition of the indigestible residue of the food, but is a product of the metamorphosis of the fluids and solids of the body itself; which seems necessarily to follow from this consideration among others,—that fæcal matter is still discharged in considerable quantity, long after the intestinal tube has been completely emptied of its alimentary contents. It has been shown by Prof. Liebig, that a substance having the characteristic odour of fæces may be artificially obtained by the imperfect oxidation of albumen, fibrine, caseine, or gelatine.

427. The foregoing are the Secreting organs, whose function seems most directly subservient to the *depuration* of the blood; but besides these, a vast number of glandular bodies are met-with in the different classes and orders of Animals, which eliminate products that have special uses in the economy, but are not in themselves excrementitious. Some of these have a very extensive diffusion; others a more limited one. Under the former head may be ranked the secreting organs which minister to the Digestive

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* The glandulæ of *Brunner* strongly resemble the Salivary glands and Pancreas in miniature; and as they are restricted to the duodenum, it is probable that their secretion takes some share, with that of the liver and pancreas, in the act of chylification, perhaps furnishing the 'succus entericus,' which seems to be scarcely less potent than the biliary and pancreatic fluids themselves (§ 165).

operation; for example, the *Gastric follicles*, the *Salivary glands*, and the *Pancreas*. The last of these is the most restricted of the three; but it is met-with (as we have seen, § 400) under a very simple form, in the highest Mollusca, and presents itself throughout the whole of the Vertebrated series, gradually advancing to a higher type of structure as we ascend the scale. The *Lachrymal* and *Mammary glands*, on the other hand, are more limited in their distribution; for the former are confined to the three higher classes of Vertebrata, and the latter to Mammalia only. Various glands for eliminating *odoriferous* matters, such as musk and castor,—or *poisonous* substances, as those connected with the 'stings' of Hymenopterous insects, contained in the mandibles of Spiders, and placed at the end of the tail of Scorpions,—or a *glutinous* matter which hardens into a thread when expressed through a narrow orifice, as that which supplies the spinnerets at the end of the abdomen of the Spider, and furnishes the material for the 'cocoon' spun by the mouth of the larva of many Insects,—are of very limited diffusion; being confined to smaller groups, and even in some instances to a particular genus or species.—The Skin of many animals, again, is abundantly furnished with *Mucous* and *Sebaceous* follicles; whose secreting action is obviously rather protective as regards the integument, than depurative as regards the blood. The Mucous secretion is generally found in aquatic animals; and prevents the water from coming into direct contact with the skin. The follicles by whose cells it is eliminated from the blood, are usually very simple in their character, resembling those of ordinary Mucous membranes (Fig. 170); but sometimes they are more complex, especially in Fishes. So the Sebaceous follicles are more commonly found in the skin of animals which live on land; and the office of their secretion appears to be, to prevent its surface from being dried-up and cracked by the action of the sun and air. It is especially abundant in those tribes which are formed to inhabit warm climates. The sebaceous glandulæ present a degree of variety as to their complexity, which is similar to that which exists among the mucous glandules; some of them being simple follicles lodged in the substance of the skin; whilst others are composed of similar follicles, more or less branched, elongated, or convoluted; and others, again, seem to consist of little else than clusters of fat-cells, out of which an excretory duct arises. In the Mammalia, they very commonly open into the hair-canal; and in Birds, into the socket of the stem of the feather. Various peculiar glands, moreover, whose uses are but little known, are connected with the genital apparatus. The Testes, or *spermatic* glands, will be described in a subsequent chapter.—In all these cases, the general plan of structure is the same; and the difference in the products can be attributed to nothing else, than to a peculiarity in the endowments of the epithelial cells which are the real instruments of the secretion.

428. *Metastasis of Secretion.*—Although the number and variety of the secretions become greater, in proportion to the increased complexity of the nutritive processes in the higher classes, and although each appears as if it could be formed by its own organ alone, yet we may observe, even in the highest animals, some traces of the community of function which characterises the secreting apparatus of the lowest. It has been shown that, although the products of secretion are so diversified, the elementary structure of all glands is the same; that wherever there is a free secreting

surface, it may be regarded as an extension of the general envelope of the body, or of that reflexion of it which lines the digestive cavity; that its epithelium is continuous with the epidermis of the integument, or with the epithelium of the mucous membrane from which it is prolonged; and that the peculiar principles of the secreted products pre-exist in the blood, in a form which is at least closely allied to that which they assume after their separation. If, then, the general law formerly stated (§ 110) be correct, we should find that, when the function of any particular gland is suspended, or when it is not performed with sufficient activity to separate all the excretory products from the blood, other secreting organs, or even the general surface, should be able to perform it in some degree. That this is actually the case, pathological observation is continually showing; and so striking are the 'metastases of secretion' which are thus exhibited, that it was even asserted by Haller that almost all secretions may, under the influence of disease, be formed by each and every secreting organ. This statement, however, needs to be received with some limitation; and it would probably be safest to restrict it to the *excretions*, whose elements pre-exist in the blood, and accumulate there when the elimination of them by their natural channel is suspended. Thus it seems to be established by a great mass of observations, that *Urine*, or a fluid presenting its essential characters, may pass-off by the mucous membrane of the intestinal canal, by the salivary, lachrymal, and mammary glands, by the testes, by the ears, nose, and umbilicus, by parts of the ordinary cutaneous surface, and even by serous membranes, such as the arachnoid lining the ventricles of the brain, the pleura, and the peritoneum; and such a metastasis has not only taken place in cases in which the normal excretion was checked or impeded by disease, but has been induced experimentally by extirpating the kidneys, or by tying the renal artery.—So, again, if the elimination of the *Bile* be checked by disease of the liver, or by the application of a ligature to the vena portæ, or if its passage out of the system be prevented by the application of a ligature to the biliary duct, some (at least) of its elements are discharged through other channels; the urine, the pancreatic fluid, the milk, the cutaneous transpiration, and even the sputa derived from the respiratory passages, being more or less deeply tinged with the yellowish-brown colouring-matter of bile, and possessing its characteristic taste; and the same matters being also found in the fluids of the serous cavities, and passing even into the solid tissues.—The secretion of *Milk*, also, has been thus transferred to different parts in the skin, to the gastro-intestinal mucous membrane, to the mucous membrane lining the bronchial tubes, and even to the surface of an ulcer.—Thus we see that those products of decomposition, at least, which accumulate in the blood when their usual exit-pipe is no longer open, may find their way through other channels; a provision which is obviously intended to diminish the injurious results of a suspension of the excretory functions (§ 394), and which is at the same time in complete and beautiful harmony with the general principle, that the specialisation of a function does not involve the complete extinction of its original generality.*

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* For a more detailed examination of this interesting topic, see the Author's article on 'Secretion' in the "Cyclopædia of Anatomy and Physiology," Vol. III.

CHAPTER X.

EVOLUTION OF LIGHT, HEAT, AND ELECTRICITY.

1. *General Considerations.*

429. It has been shown in the preceding Chapters, that whilst the existence of the *Vegetable* world depends upon the constant agency of certain physical forces (Light and Heat), by which the germ is enabled to draw-in and to appropriate the inorganic elements, which it combines into organic compounds, and incorporates with itself into an organised fabric,—that of the *Animal* kingdom is rather dependent upon the supply of food which it derives from the vegetable world, by means of which its higher forms (at least) are rendered comparatively independent of external agencies, requiring no Light to enable them to appropriate their aliment, and being able to generate within themselves the Heat which is necessary to sustain their vital activity. In the production of *Heat,* then, we have one of those cases in which Animals restore to the Physical Universe the Forces which it has imparted to Plants (General Physiology); and we shall find it to be effected by the very act of restoring to the condition of inorganic matter, those elements which the agency of Light and Heat upon the vegetable germ had enabled it to withdraw. Although the production of Heat is most considerable and regular in those higher animals which are termed warm-blooded, yet it takes place in an inferior degree probably in all. It is also a phenomenon of occasional occurrence in Plants, but only under the same conditions as in Animals, *viz.* when Organic compounds are being partially or completely restored to the condition of Inorganic matter; and it would seem as if it was in them rather a necessary result of transformations which are being effected for other purposes, than a purpose for which such transformations are to be made.—The same may be said of the production of *Light.* It is by no means an ordinary phenomenon in the Animal kingdom; but where it does occur, it appears to have some special purpose; and although the processes by which it is maintained are not clearly understood, yet there can be little doubt that it too is dependent upon a slow combustion, in which the carbon and hydrogen of the living system are given-back to the atmosphere as carbonic acid and water; the oxidation of other substances, also, perhaps contributing to the effect. On the other hand, its appearance in Plants is a much rarer occurrence, and seems to be (so to speak) accidental.—Of the generation of *Electricity,* we know comparatively little. There is strong evidence that its production must be going-on, in every action of Organic as well as of Inorganic Chemistry; and that a disturbance of electric equilibrium must be continually taking-place in each molecule of the living Plant and Animal. But it would seem as if, in general, the generation of electricity is simply a result of changes which are directed to other ends; and that, so far from any use being made of it in the

economy, there is usually a set of provisions for the speediest possible restoration of the disturbed equilibrium. In certain Animals, however, the case is very different; for we find them endowed with an apparatus whose special purpose is obviously the generation of Electricity, in considerable amount and intensity; and although we may not be acquainted with all the objects which this curious organisation may answer, yet some of its more obvious uses can be clearly made-out.

2. *Evolution of Light.*

430. *Evolution of Light in Vegetables.*—It has been asserted that many flowers, especially those of an orange colour, such as the *Tropæolum majus* (Nasturtium), *Calendula officinalis* (Marigold), *Helianthus annuus* (Sun-flower), &c., disengage light in serene and warm summer evenings, sometimes in the form of sparks, sometimes in a more feeble and uniform manner; but many physiologists are disposed to question these assertions, from their not having been themselves able to witness the phenomena. There is no doubt, however, that light is emitted by many *Fungi*, whilst actively vegetating, and in some instances to a very considerable extent.* The light is perceived in all parts of the plant, but chiefly in the young white shoots; and it is more vivid in young than in old plants. The phosphorescence is stronger in such as grow in the moist and warm localities of mines, than in those inhabiting dry and cold situations. It ceases if the plant be placed in vacuo, or in any atmosphere which does not contain oxygen; but reappears when it is restored to the air, even after remaining for some hours in vacuo or in azote. No phosphorescence is perceived after the death of the plant. Some *Algæ*, also, have been observed to be luminous when in a growing state.—On the other hand, luminosity is sometimes observed under circumstances that forbid our regarding it as in any degree a vital phenomenon. Thus it is stated by Martius, that the juice of the *Euphorbia phosphorea*, a Brazilian plant, emits light, especially when heated. An evolution of light has frequently been observed to take place from dead and decaying wood of various kinds, particularly that of roots; it seems connected with the conversion of oxygen into carbonic acid, but it is not increased when the substance is placed in pure oxygen. Decomposing Fungi, also, frequently exhibit luminosity; but this is very different from that displayed by some of the

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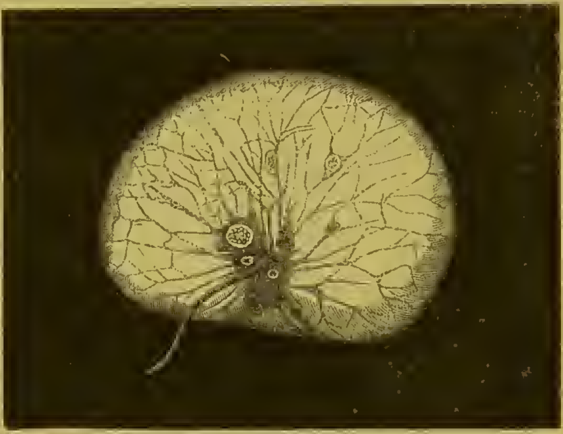
* The following is one of the most recent and authentic instances yet recorded.—"One dark night, about the beginning of December, while passing along the streets of the Villa de Natividada, I observed some boys amusing themselves with some luminous object, which I at first supposed to be a kind of large fire-fly; but on making inquiry, I found it to be a beautiful phosphorescent Fungus, belonging to the genus Agaricus; and was told that it grew abundantly in the neighbourhood, on the decaying leaves of a dwarf-palm. Next day I obtained a great many specimens, and found them to vary from one to two-and-a-half inches across. The whole plant gives out at night a bright phosphorescent light, of a pale greenish hue, similar to that emitted by the larger fire-flies, or by those curious soft-bodied marine animals, the Pyrosomæ. From this circumstance, and from growing on a palm, it is called by the inhabitants 'Flor do Coco.' The light given out by a few of these Fungi in a dark room was sufficient to read by. I was not aware at the time I discovered this fungus, that any other species of the same genus exhibited a similar phenomenon; such, however, is the case in the *Ag. olearius* of De Candolle; and Mr. Drummond of Swan River Colony in Australia has given an account of a very large phosphorescent species occasionally found there."—Gardner's "Travels in Brazil," 2nd ed. p. 264.

same tribe during their living state.—Considering that in all the circumstances mentioned, the combination of carbon and oxygen is taking place to some amount, it seems difficult to believe that there is not some connection between the phenomena; but no speculation can yet be raised on the subject, with any prospect of stability, from the want of sufficient facts as its basis.

431. *Evolution of Light in Animals.*—A large proportion of the lower classes of aquatic Animals possess the property of luminosity in a greater or less degree. The 'phosphorescence of the sea,' which has been observed in every zone, but more remarkably between the tropics, is due to this cause. When a vessel ploughs the ocean during the night, the waves,—especially those in her wake, or those which have beaten against the sides,—exhibit a diffused lustre, interspersed here and there by stars or ribands of more intense brilliance. The uniform diffused light is partly emitted by innumerable minute Animals, which abound in the waters of the surface; and these, if taken-up into a glass vessel, continue to exhibit it, especially when the fluid is agitated. The most common source of the *diffused* luminosity, is a minute nearly globular animal, provided with a stalk-like appendage, which has received the appellation of *Noctiluca miliaris** (Fig. 188). To the naked eye, the body presents the appearance of a minute lump of homogeneous jelly; when examined microscopically, it is found to consist of a sac with definite walls, having its interior, which is for the most part filled with fluid, traversed by a network of a more consistent gelatinous substance, containing numerous *vacuolæ*, the size and form of which are continually undergoing alteration. Altogether, its zoological position seems to be in the group of *Rhizopoda* (§ 35), though it differs from the ordinary forms of that group in several important particulars. The light may proceed from the whole of the body at once, or from parts of it, passing in succession from one to another; there is, therefore, no special organ for its production in these animals. When the source of the luminosity is carefully examined, it is found that what appears to the eye to be a uniform glow, is resolvable under a sufficient magnifying power into a multitude of evanescent scintillations; differing in this respect from the steady lustre of the luminous Insects (§ 435). It does not appear that the light proceeds from any phosphorescent secretion, which can be separated from the animals; nor does its emission seem to be dependent upon a combustive process, for which the

Fig. 188.



Noctiluca Miliaris.

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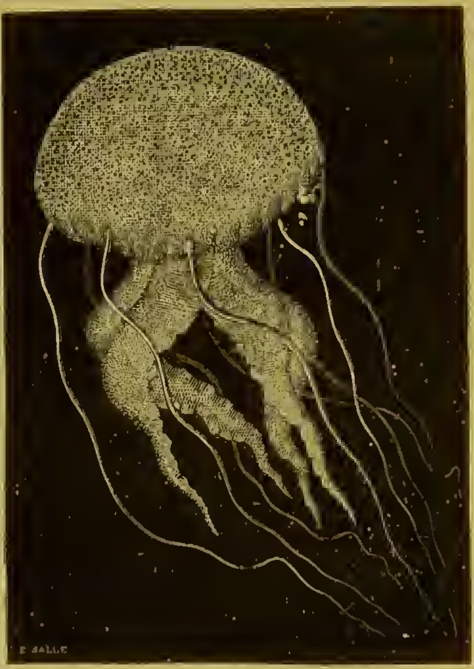
* The Structure and Luminous phenomena of this animal have been peculiarly well studied by M. de Quatrefages ("Ann. des Sci. Nat." 3e Sér. Zool., Tom. XIV., pp. 226, *et seq.*). See also Dr. Pring's experimental inquiries, in "Philosophical Magazine," Dec. 1849.

contact of oxygen is necessary. On the other hand, various physical agents which tend to excite contraction of the tissues of the animal, augment for a time its luminosity. This is the case, for example, with pressure; and it is thus that the breaking of the waves on the shore is marked by lines of brilliant light, or that agitation of a tube containing Noctilucæ swimming in water causes their phosphorescence to be developed, and to be displayed with augmented intensity for some time. It has been found by Dr. Pring, that when the water containing Noctilucæ was subjected to a simple galvanic current, no very perceptible effect could be observed; but when an electro-magnetic current was employed, after a time a steady and continued flow of light was given-out from the whole of the water, the surface of which appeared as if spangled with numberless minute but persistent points of light; the light ceased after a quarter of an hour, and could not be reproduced, evidently in consequence of the death of the animals. With very dilute sulphuric acid, the contraction is strongly marked, being attended with a rupture (more or less rapid) of the filaments uniting the interior gelatinous mass to the envelope, and finally with a complete detachment of this mass, which escapes from the envelope, leaving it empty. At the first contact of the dilute acid with the *Noctilucæ*, there is given out a very brilliant light, which becomes fixed in one spot; and consentaneously with the rupture of the fibres and with the disorganization of the interior mass (which proceed from their permanent contraction), the clear white light spreads over the body, until the whole resembles a ball of silver. The brilliancy soon diminishes, however, and somewhat rapidly disappears. Similar effects are produced by other acids, as well as by other irritating fluids. On the other hand, agents which tend immediately to depress the vital powers, occasion the speedy extinction of the light. Thus Dr. Pring found that when sulphuretted hydrogen was passed into water containing *Noctilucæ*, it instantly destroyed their luminosity, being at once fatal to the animals. With carbonic acid, the luminous property of the water was strongly and continuously brought out for about fifteen minutes, the light being bright enough to enable the hands of a watch to be seen in a dark room; but at the expiration of that time the light gradually became fainter, and in five or ten minutes more it had totally ceased. A few drops of ether let-fall into the sea-water in the dark, appeared instantly to deprive it of its luminous property. On substituting chloroform for ether, in a second experiment, a very bright and persistent phosphorescence was given-out for a few minutes, after which the water speedily became dark, the animals being evidently destroyed.—Some other Protozoa, belonging to the class of *Infusoria*, are stated to possess the attribute of luminosity.

432. In the class of *Zoophytes*, the phenomenon seems to be not uncommon among the members of the order *Hydroida;* being most distinctly seen when the animals are in a state of vigour, and are subjected to some shock or irritation. It is most remarkably exhibited, however, by the several species of the family *Pennatulidæ*, belonging to the order *Asteroida;* but their phosphorescence seems to be only displayed under the influence of some mechanical or chemical irritation. It has been observed by Prof. E. Forbes, that when any portion of the stem or branches of a Pennatula is touched, the luminosity first shows

itself there, and then spreads itself, in a wave-like manner, towards the polypiferous extremities; whilst, if any of these extremities be touched, the luminosity does not spread backwards from the point of contact, but remains confined to the part irritated. When plunged into fresh water, the Pennatula scatters sparks about in all directions, and then ceases to be luminous; but when plunged into spirits, it does not do so, but remains phosphorescent for some minutes, the light dying gradually away, and vanishing last of all from the uppermost polypes.*—Of all Radiated animals, however, the *Acalephæ* are most distinguished by this endowment; a large proportion of them being more or less phosphorescent, especially in tropical regions, where the most brilliant luminosity is displayed. The light is emitted, particularly round the tentacula, and from the ciliated surfaces, during the movements of the animal: and it seems to proceed from a mucus secreted from the integument, which may continue to exhibit the same property for a time when removed from it. This mucus, which has a very acrid character when applied to the human skin, communicates to it a phosphorescent property; and, when mixed with water or milk, it renders these fluids luminous for some hours, particularly when they are warmed and agitated. From this source it is probable that the diffused phosphorescence of the sea is partly derived; whilst the brilliant stars and ribands, with which the surface is bespangled, indicate the presence of the living tenants of the deep.—Certain *Echinodermata,* also, have exhibited luminosity; but the phenomenon seems to be restricted to the orders *Asteriada* and *Ophiurida.*

Fig. 189.



Pelagia noctiluca.

433. Each class of the Molluscous series, also, contains phosphorescent animals; but the phenomenon is especially frequent in the class of Tunicata, in which, however, it appears to be chiefly or entirely restricted to the families *Salpidæ* and *Pyrosomidæ,* which float freely on the waters of the ocean, abounding especially in the warmer seas. Of these, too, it may be observed that the luminosity is augmented by agitation or by friction. Among the Conchifera, this phenomenon has been chiefly witnessed in the *Pholas* and *Lithodomus.* No marine Gasteropod has yet been noticed to possess luminosity; but phosphorescence has been observed in a species of Slug (*Phosphorax noctilucus*) inhabiting the higher mountains of Teneriffe. Among Pteropods the *Cleodora,* and among Cephalopods the *Octopus,* have been seen to exhibit

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* See Dr. Johnston's "British Zoophytes," pp. 25–27, 150–155.

phosphorescence. In all these, the general phenomena are analogous; the luminous matter appearing to be a secretion from the surface of the animals, which communicates its peculiar property to water or to solid substances that come in contact with it. The light disappears in vacuo, but reappears in air; it is increased by moderate heat, and by gently stimulating fluids; whilst a cold or boiling temperature, or strong stimulants, soon extinguish it. It continues for some days after death, but ceases at the commencement of putrefaction.—The same power has been attributed to *Fishes;* but it is not improbable that, with regard to these, there has been a partial deception, arising from the excitement given by their movements to the sources of phosphorescence in the surrounding water. Late observations, however, lead to the belief that, in some species of Fish, there is an inherent luminosity: a species of *Scopelus,* three inches long, has been seen to emit a brilliant phosphorescent light, in stars or spangles, from various parts of the scaly covering of the body and head; and this continued to be displayed at intervals during the life of the animal, in a glass of sea-water,—ceasing entirely with its death.

434. Among the Articulated classes, the evolution of light is by no means an uncommon phenomenon; but in some of these it appears due to a different agency from that on which the luminosity of Zoophytes and Mollusks is dependent. The luminosity which is observable in many of the marine *Annelida* is not a steady glow, but a series of vivid scintillations (strongly resembling those produced by an electric discharge through a tube spotted with tin-foil) that pass along a considerable number of segments, lasting for an instant only, but capable of being repeatedly excited by any irritation applied to the body of the animal. The peculiar character of this emission of light seems to remove it altogether from the category of ordinary 'phosphorescence,' and leads to the supposition that it is dependent upon a direct conversion of Vital Force into Light.* A very similar kind of luminosity is observable in many minute Crustacea, which emit light in brilliant jets; and it is a curious fact, mentioned by Prof. E. Forbes, that the cavity of Salpæ which have been deprived of their visceral 'nuclei' (Fig. 122, A, *c*), often contains multitudes of minute Crustacea, which give out such a succession of phosphorescent flashes, as possibly to deceive the observer into the belief that it is the mollusk itself which is luminous.

435. Among *Insects,* however, we find numerous examples of a luminosity which is obviously of a different character, being clearly traceable to a combustive process; and this is restricted to particular portions of the body, sometimes even to minute points. The luminous Insects are most numerous among the order *Coleoptera* (Beetle tribe); and are nearly restricted to two families, the *Elateridæ,* and the *Lampyridæ.*† The

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* This was the conclusion at which the Author had arrived from his own observations upon the luminosity of the Annelida, made at Tenby in the year 1843. About the same time, M. de Quatrefages arrived at similar conclusions from his observations on the Annelida of La Manche. See his Memoirs in the "Ann. des Sci. Nat." 2e Sér. Zool., Tom. XIX., and 3e Sér. Tom. XIV.—See also the Author's "Principles of General Physiology," and his Memoir on the 'Mutual Relations of the Vital and Physical Forces' in "Philos. Transact.," 1850.

† Of the reputed luminous power of the *Fulgora*—a very remarkable genus of the order *Homoptera,* of which one species inhabits Guiana, whilst another is a native of China,—

former contains about 30 luminous species, which are all natives of the warmer parts of the New World. The light of these 'Fire-flies' proceeds from two minute but brilliant points, which are situated one on each side of the front of the thorax; and there is another beneath the hinder part of the thorax, which is only seen during flight. The light proceeding from these points is sufficiently intense to allow small print to be read in the profoundest darkness, if the insect be held in the fingers and moved along the lines. In all the luminous insects of this family, the two sexes are equally phosphorescent.—The family *Lampyridæ* contains about 200 species known to be luminous, the greater part of which are natives of America, whilst others are widely diffused through the Old World. These are known as 'Glow-worms' (*Lampyris noctiluca and Lam. splendidula*); their light issues from the under surface of the three last abdominal rings; it is most brilliant in the female, and exists in a feeble degree in the egg, larva, and chrysalis. The luminous matter consists of little granules, and is contained in minute sacs, covered with a transparent horny lid. These sacs are mostly composed of a close net-work of finely-divided tracheæ; which also ramify through every part of the granular substance. The lid exhibits a number of flattened surfaces, so contrived as to diffuse the light in the most advantageous manner. The phosphorescence appears to be occasioned by the slow combustion of a peculiar organic compound, the production of which is dependent for its continuance upon the life and health of the animal; the activity of this combustion is stimulated by anything which excites the vital functions of the individual, and it is particularly influenced by the energy of the respiratory process. If the opening of the trachea which supplies the luminous sac, be closed, so as to check the access of air to its contents, the light ceases; but if the sac be lifted from its place, without injuring the trachea, the light is not interrupted. In all active movements of the body, in which the respiration is energetic, the light is proportionably increased in brilliancy. If the luminous segments be separated from the rest of the body, they continue phosphorescent for some time; and if they be crushed between the fingers, long streaks of light are perceived to issue from the yellowish matter which they contain. By careful experiments upon the luminous product thus separated from the body, Prof. Matteucci has been able to prove that the emission of light is dependent upon a combustive process, in which carbonic acid is rapidly generated at the expense of the surrounding oxygen; and he has also ascertained by analysis, that the luminous matter does not contain any appreciable quantity of phosphorus.*—Phosphorescence is a rare phenomenon among aerial animals of the higher classes. An emission of light has been seen from the egg of the grey lizard; and it has been stated that a species of Frog or Toad inhabiting Surinam is luminous, especially in the interior of its mouth. (See § 437.)

436. Of the particular objects of this provision in the animal economy,

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there is, to say the least, very considerable doubt. The authority on which it has been asserted (that of Madame Merian), is a very questionable one; and naturalists who have themselves carefully observed these insects, have seen no traces of it. There may, however, be some ground for the statement; particularly if, as has been suggested, the luminosity be exhibited by one sex only, and during only a portion of the year.

[*] "Lectures on the Physical Phenomena of Living Beings," p. 181.

little is known, and much has been conjectured. It is generally imagined, that it is destined to enable the sexes of the nocturnal animals (especially Insects) to seek each other for the perpetuation of the race; and this hypothesis would seem to derive support from the fact, that the light is generally most brilliant at the season of the exercise of the reproductive function, and at that period exists in some species (such as the Earth-worm) which do not manifest it at any other. Moreover it is well-known that the male Glow-worm, which ranges the air (whilst the female, being destitute of wings, is confined to the earth), is attracted by any luminous object; so that the poetical language of Dumeril, who regards the phosphorescence of the female as "the lamp of love—the pharos—the telegraph of the night, which scintillates and marks in the silence of darkness the spot appointed for the lovers' rendezvous," would not seem so incorrect as the ideas of Poets on subjects of Natural History usually are. It may be objected on the other hand, that there are many moths and beetles, which have a similar tendency to fly towards the light, and among which no phosphorescence is exhibited. Some of these, however, are faintly luminous; and it would not seem improbable that the Insects which are attracted by flame, and thus show that they are seeking for objects which emit light, may be cognizant of more feeble degrees of its emission, than our eyes can appreciate.* Still it must be remembered that certain animals (as Zoophytes) are phosphorescent, which have no occasion to seek each other with this object; and it does not seem impossible that the property may be conferred upon them (like the stinging power possessed by some) as a means of self-defence, in the deficiency of active powers of locomotion, or of dense external covering. It may serve, too, for the illumination (however faintly) of those depths of the ocean, which are known to be tenanted by Fishes and other marine tribes, but which receive no appreciable portion of solar light.

437. An evolution of Light during the incipient decay of dead animal matter, is by no means of uncommon occurrence. It has been most frequently observed to proceed from the bodies of Fishes, Mollusca, Medusæ, and other marine tribes; but it has been seen also to be evolved from the surface of terrestrial animals, and even of Man. This phosphorescence ceases immediately on the commencement of fœtid putrefaction; and it would appear to proceed from the formation of luminous matter during an early stage of decomposition, by some of those primary changes in the combination of the organic elements, which immediately succeed dissolution, or which may even precede it for a brief period. Such would

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* It has been objected that, as the male is somewhat luminous, and also the larva and pupa, the meeting of the sexes can scarcely be the object of the provision. But this difficulty is easily surmounted. Mr. Kirby justly remarks, that "as the light proceeds from a peculiarly-organised substance, which probably must be in part elaborated in the larva and pupa states, there seems nothing inconsistent in the fact of *some* light being then emitted, with the supposition of its being destined solely for use in the perfect state. And the circumstance of the male having the same luminous property, no more proves that the superior brilliancy of the female is not intended for conducting him to her, than the existence of nipples and sometimes of milk in man proves that the breast of woman is not meant for the support of her offspring." The luminosity of the Insect in all these states may have the more remote purpose, also, of making its presence known to the nocturnal birds, &c. which are destined, in the economy of nature, to feed upon it. The larva of the *Lampyris occidentalis* has been observed, when alarmed, to feign death and extinguish its light.

seem to have been the case in certain well-authenticated instances of the evolution of light in the living Human subject.* In most of these cases, the individuals exhibiting the luminosity had suffered from some wasting disease, and were near death. One instance is recorded, in which a large cancerous sore of the breast emitted light enough to enable the hands of a watch-dial to be distinctly seen, when it was held within a few inches of the ulcer; here, too, decomposition was obviously going-on, and the phosphorescent matter produced by it was exposed to the oxygenating action of the atmosphere.†

3. *Evolution of Heat.*

438. As it is a part of the peculiar character of living organised beings, that their vital activity can only be sustained under the constant influence of Heat, it is obvious that those only can be rendered independent of variations in the temperature of the surrounding medium, so as to maintain that which is most favourable to the performance of their various actions, which have the power of *generating* Heat, when it is not sufficiently imparted to them from external sources, and of *resisting* its influence, when it is excessive. Having already considered the means by which the temperature of the living body is kept *down* to its proper standard (CHAP. VII.), we have now to enquire into the sources of that generation of Heat, within the living body, which keeps *up* its temperature in 'warm-blooded' animals to a certain fixed point, and which assists in enabling even the 'cold-blooded' to resist the effects of extreme depression of the external temperature.—It is well known that almost all Chemical changes are attended with some disturbance in the temperature of the agents concerned; and it might not unreasonably be surmised that, of those which are so constantly occurring in the living system, some may be connected with the disengagement of the Heat peculiar to it. Much uncertainty still prevails on this subject; but there can be little doubt that a large proportion of the caloric liberated by organised beings, is generated by the combination of atmospheric oxygen with the carbon and hydrogen furnished by them, to form the carbonic acid and water which they are constantly excreting; since we find these two changes everywhere bearing a close relation with each other. Several other changes of composition are going-on, however, in the living body, to which a part of the effect must be attributed; and there are some residual phenomena,

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* "An account of several cases of the Evolution of Light in the Living Human Subject;" by Sir Henry Marsh, M.D., M.R.I.A., &c.

† Such facts appear to give support to the idea, that a *preternatural combustibility* may sometimes exist in the body, owing to the retention of phosphorus-compounds, which should normally be excreted from it by the urine after undergoing oxidation. It has been observed that the *breath* of drunkards has sometimes exhibited luminosity, as if it contained the vapour of phosphorus or of some of its compounds; and it has been found by experiments upon dogs, that if phosphorus be mixed with oil and injected into the blood-vessels, it escapes unburned from the lungs. ("Casper's Wochenschrift," 1849, No. 15.)—The Author has seen the narration of a case, drawn-up by the subject of it (a highly respectable Clergyman), in which a troublesome sore, occasioned by the combustion of phosphorus on the hand, twice at distant intervals emitted a flame which burned the surrounding parts. It was particularly stated that ignition could not have been effected by any neighbouring flame, and that the combustion could not be due to any particles of phosphorus remaining in the wound; and it does not seem improbable that, in the peculiar condition of the sore, an unusual amount of phosphorus-compounds had been deposited in it, so as even to become spontaneously inflammable on the contact of oxygen.

which seem to indicate that Heat may occasionally be a direct product of the metamorphosis of the Nervous Force (§ 453).

439. *Evolution of Heat in Vegetables.*—Much dispute has occurred at different periods, as to whether Plants could be considered as having a *proper heat* or not; and this has resulted from the limited view which has been taken of the processes of the Vegetable Economy. Although the excretion of Carbonic acid is constantly going-on, under the conditions formerly described (§ 270), it usually takes place so slowly, and from a surface so openly exposed to the atmosphere, that it could scarcely be expected that there should be any sensible elevation of the temperature of the part from this source,—especially when it is considered that a constant loss of heat is taking place by evaporation : and as there is no provision for the conveyance of caloric set-free in one part, to distant portions of the system, a *general* maintenance of vital warmth would be still less anticipated. In plants of small or moderate size, accordingly, the temperature is found to vary with that of the atmosphere; but the interior of large trunks seems to maintain a more uniform degree, being colder than the atmosphere in summer, and warmer in winter. This fact may be accounted-for on two different grounds. The slow conducting power of the wood, which is much less transversely to the direction of its fibre, than with it,* would prevent the interior of a large trunk from being rapidly affected by changes in the heat of the external air; and accordingly, it is found that, the larger the trunk on which the observation is made, the greater is the difference. Again, some motion of the sap takes place even in winter; and as the earth, at a few feet below the surface, preserves a very uniform temperature, it is not improbable that the transmission of fluid derived from it through the stem, may have an influence on the state of the latter; a supposition which is countenanced by the fact, that the temperature of the interior of a large trunk, and that of the soil four feet below the surface (which may be regarded as the medium depth of roots), bear a very close correspondence. It is reasonable to suppose that both these causes may be in operation.—By experiments, however, made with instruments of great susceptibility to changes of temperature, Dutrochet ascertained that Plants do possess some power of generating heat, in the parts in which the most active changes are taking place. In order to obtain unexceptionable evidence to this effect, it was necessary to exclude the influence of evaporation in depressing the temperature. This was effected by making the comparison, not between the temperature of the plant and that of the surrounding air, but between similar parts in a living plant, and in one recently killed by immersion in hot water, which would be (after cooling) equally susceptible with the former of the diminution of temperature which evaporation causes. In some instances, this source of error was still further guarded-against, by the immersion of both plants in an atmosphere saturated with aqueous vapour. The temperature of the leaves and young shoots was ascertained, in preference to that of the stem; both in order to avoid the source of fallacy already mentioned, and because in them the greatest *proper heat* might be expected. With these precautions, the result was constantly the same. An elevation of temperature, sometimes to the amount of

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* See Dr. Tyndall, in "Philos. Transact.," 1853, p. 226.

nearly a degree (Fahr.), was observed in the herbaceous parts of actively-growing plants; differing with the species, the energy of vegetation, and the time of the day. The highest temperature is observed about noon; it increases previously, and afterwards diminishes. This diurnal change is partly influenced by that of the Light to which the plant is exposed.*

440. It is, however, when the processes of vegetation give rise to an extraordinary liberation of Carbonic acid (§ 274), that the evolution of heat becomes manifest. This is the case during Germination, when the elevation of temperature, scarcely manifested by a single seed, becomes evident if a number are brought together, as in the process of malting, in which the thermometer has been seen to rise to 110°.—The same may be said of the other period of vegetable growth, in which the function of respiration is carried-on to a remarkable extent; that of Flowering. From the large surface exposed, it is evident that, in by far the greater number of instances, the heat will be carried-off by the atmosphere, the instant it is developed; nevertheless the flowers of a Cistus showed a temperature of 79° whilst the air was at 76°, and those of a Geranium 87° when the air was at 81°. It is in plants of the Arum tribe, however, where flowers are collected in great numbers within cases which act as non-conductors, that the elevation of temperature becomes most appreciable; and it bears a definite relation with the quantity of oxygen converted into carbonic acid. Thus a thermometer placed in the centre of five spadixes of the *Arum Cordifolium* has been seen to rise to 111°, and in the centre of twelve to 121°, while the temperature of the external air was only 66°; but the production of heat was wholly checked, by preventing the spadix from coming in contact with the air.—The truth of statements of this sort, which has been questioned by many physiologists, has been placed beyond all doubt by the observations of M. Ad. Brongniart. He found that, at the first opening of the spathe of *Colocasia odora*, the temperature of the spadix was 8·1° above that of the surrounding air; that this increased during the next day to 18°; and, during the emission of the pollen on the three succeeding days, to 20°; after which it began to diminish with the fading of the flower. More recently these observations have been confirmed by MM. Vrolik and Vriese; who have added to them some important facts. The rise of the temperature was found to be more rapid and considerable, in a spadix placed in oxygen, than in one at a corresponding stage surrounded by common air; and a larger proportion of carbonic acid gas was evolved. On the other hand, when a spadix, of which the flowers had already begun to expand, and the temperature to rise, was placed in nitrogen, the temperature sank, and exhibited no elevation during the emission of the pollen; nor was any carbonic acid evolved.† The correspondence between the evolution of heat and the consumption of oxygen is made yet more clear by the observations of M. Garreau,‡ who has noted the temperature of these spadixes, hour by hour, during the 'paroxysm' of flowering, and the quantity of oxygen consumed during the same periods, with the following result;—the amount of heat developed being expressed by the number of degrees (Cent.) shown by the thermometer above the temperature of the surrounding air, and the quan-

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[*] "Annales des Sci. Nat.," 2e Sér., Botan., Tom. XII.

[†] Op. cit., 2e Sér. Tom. XI.

[‡] Op. cit., 3e Sér., Tom. XVI., p. 250.

tity of oxygen consumed being stated in multiples of the volume of each spadix :—

	No. 1.		No. 2.		No. 3.	
	Heat produced.	Oxygen consumed.	Heat produced.	Oxygen consumed.	Heat produced.	Oxygen consumed.
1st hour	3·2	11·1	4·2	16·5	3·5	10·0
2nd hour	5·3	16·2	7·2	21·1	6·1	15·5
3rd hour	7·8	21·4	9·8	27·7	8·6	21·1
4th hour	8·3	28·5	8·4	18·9	10·2	31·1
5th hour	6·0	14·2	4·8	12·2	9·8	18·9
6th hour	2·7	5·7	2·7	5·5	5·7	7·7
Mean	5·5	16·1	6·1	16·9	7·3	17·3

441. *Evolution of Heat in Animals.*—Although we find many instances in the Animal kingdom, in which the capability of maintaining an elevated and uniform temperature is exhibited in a degree to which nothing comparable exists in plants, yet this is by no means a *constant* function of animal, any more than of vegetable organisms. Among the lower tribes of Animals, in which the power of locomotion is but feeble, and the supply of the wants of the system not immediately dependent upon it, very little more heat is generated than in Plants. But wherever a high degree of muscular energy is required, in connection with a general activity of the functions of the nervous system, the evolution of caloric to a remarkable extent is provided-for in the nutritive processes. We may regard it, therefore, as in *its degree* essentially connected with the development of the Animal powers relatively to the system of Organic life; although really *dependent*, as it would appear, upon the changes occurring in the latter. —It is worthy of notice that, although the temperature of the various parts of the Animal body is usually much more uniform than that of the different organs in Vegetables (owing to the comparative rapidity with which the general circulation of the former diffuses the heat evolved in any one part, and thus tends to equalise the whole), wherever processes are going-on which call the nutritive functions into extraordinary activity, *there* a corresponding elevation of temperature occurs. Thus, a slightly increased evolution of heat from the Stomach has been observed, during that determination of blood to its capillaries, which takes place during digestion; the same is observable in the Generative organs of many animals, in which the aptitude for the function is periodic only; and the temperature of a Muscle (as ascertained by MM. Becquerel and Breschet) rises a degree or more during its contraction.

442. Our knowledge of the heat evolved by the lower Invertebrata is very limited. The *Infusoria* have been observed to possess a certain degree of power of resisting cold. When the water containing them is frozen, they are not at once destroyed; but each lives for a time in a small uncongealed space, where the fluid seems to be kept from freezing by the caloric liberated from the animalcule. What is known in regard to other classes, is principally derived from the experiments of John

Hunter. He found that a thermometer, introduced in the midst of several *Earthworms*, stood at 58½°, when the temperature of the external air was 57°; and in another instance, when the atmosphere was at 55°, the worms were at 57°. The amount of heat manifested by *Leeches* appeared to be nearly the same, viz. from one to two degrees above that of the atmosphere. Of the Mollusca, nearly the same may be said. Hunter found that the black slug (*Limax ater*) exhibited a temperature of 55¼°, when that of the atmosphere was 54°; and the garden snail (*Helix pomatia*) has been observed by others to evolve about the same amount of heat. Further experiments, however, are desirable, for the purpose of ascertaining whether the power of generating caloric varies in such animals with different degrees of external temperature; or whether the heat of their bodies always bears the same close relation with that of the medium in which they exist. The experiments of Hunter furnish the only information on this subject which we possess. He put several Leeches into a bottle which was immersed in a freezing mixture, and the ball of the thermometer being placed in the midst of them, the quicksilver sunk to 31°; by continuing the immersion for a sufficient length of time to destroy life, the quicksilver rose to 32°, and then the leeches froze. A similar result was obtained with a Snail. It would appear, therefore, that these animals have the power of resisting, *for a time*, the physical effects of cold; but how far this resistance is due to the power of generating heat, or to the causes arising from their structure (as in Vegetables, § 439), cannot be determined without further inquiries. The simple maintenance of a temperature equal to that of the atmosphere, by an animal whose body has a soft surface exposed to the air, implies a certain degree of power of generating caloric; since that surface (as in plants) is constantly being cooled by the evaporation of its moisture.

443. In many Vertebrated animals, the heat of the body is almost equally dependent upon that of the surrounding medium. Thus *Fishes* in general do not seem capable of maintaining a temperature more than two or three degrees higher than that of the water in which they live. There are, however, some remarkable exceptions; for Dr. J. Davy found that certain marine fishes, as the Bonito and Thunny, whose gills are supplied with nerves of unusual magnitude, and which have also a very powerful heart, and a quantity of red blood sufficient to give the muscles a dark red colour, maintain a temperature much higher than that of the white fishes of fresh water on which Hunter experimented. Thus, Dr. D. observed in the bonito a temperature of 99°, whilst that of the sea was but 80½°. Although the conditions of existence in Vertebrata, in which the animal powers are developed to their greatest extent, might have seemed to require a greater power of generating heat than Fishes usually possess, it is to be remembered that this class is less liable than those which inhabit the air, to suffer from alternations of temperature connected with the seasons. In climates subject to great atmospheric changes, the heat of the sea is comparatively uniform through the year, and that of deep lakes and rivers is but little altered. Many have the power of migrating from situations where they might otherwise suffer from cold, into deep waters; and it is an unquestionable fact, that the species which are confined to shallow lakes and ponds, and which are thus liable to be frozen during the winter, are frequently endowed with tenacity of life, sufficient to

enable them to recover after a process which is fatal to animals much lower in the scale. Fishes are occasionally found imbedded in the ice of Arctic Seas; and some of these have been known to revive when thawed.

444. In *Reptiles*, the power of generating caloric is somewhat greater. In all cases, however, the temperature of their bodies is greatly dependent upon that of the medium which they inhabit; but in proportion to the depression of the latter, do they seem endowed with the power of maintaining their own above it. Thus, when the air was at 68°, a *Proteus* manifested the same degree of heat; but when the air was lowered to 55°, the temperature of the animal was 65°. In the same manner, it appeared that the edible frog (*Rana esculenta*) possessed a temperature of 72½°, when examined in an atmosphere of 68°; and that in ice of 21°, the animal maintained a heat of 37½°. The *Chelonia* do not seem endowed with the power of evolving heat, to the same degree with the *Saurian* and *Ophidian* reptiles. In some of the more agile of the Lizard tribes, the high temperature of 86° has been noticed, when that of the external air was but 71°.—In all experiments on the influence of *change* of temperature on such animals, it is necessary to guard against the fallacy arising from the slowness (resulting from their non-conducting power) with which their bodies acquire the altered heat of the medium, whether it be increased or diminished. By attending to this precaution, it has been shown that many of the statements which have been made regarding their power of modifying their temperature, are liable to exception; but it cannot be questioned that Reptiles have some capability of generating heat, which is called into action in resisting the depressing influence of cold. This is unequivocally proved by the fact, that Frogs will remain alive in water which is frozen around them (even when the thermometer has fallen to 9°), the water in contact with the body remaining fluid, and the temperature of the body being 33°.*

445. The classes of animals, which are especially endowed with the power of producing and maintaining heat, are Insects, Birds and Mammalia. The temperature of *Insects* has been very ably investigated by Mr. Newport.†—In the *Larva* condition, the temperature of the animal corresponds much more closely with that of the atmosphere, than in the perfect state; thus, the larva of the higher species of *Hymenoptera* (Humble-bees, &c.) is usually from 2° to 4° above the surrounding medium, whilst the perfect Insect has a range of from 3° to 10°, or even more; and the caterpillar of the *Lepidoptera* is seldom more than from ½° to 2° warmer than the atmosphere (the amount varying in close relation with the activity of the individual), whilst the perfect Insect is, when much excited, 5° or 9° above it. It is probable that in those tribes, in which no complete metamorphosis exists, but in which the difference between the development of the larva and that of the perfect insect is but trifling, there is not the same variation with regard to the production of heat.—The *Pupa* state being, in all Insects which undergo a complete metamorphosis, a condition of absolute rest, the temperature of the individual is in general lower than at any previous or subsequent period of its existence; and it is only equal to, or at most very little above, that

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* On this subject, see Duméril, 'Recherches Expérimentales sur la Température des Reptiles,' in "Ann. des Sci. Nat.," 3e Sér., Tom. XVII., p. 5.

† "Philosophical Transactions," 1837.

of the surrounding medium. But in those species, which, not undergoing a complete metamorphosis, continue active during the whole of life, this diminution of the power of maintaining heat probably does not occur. Within a short period after the first change, however, the Pupa often retains some of the characteristics of the larva state, and exhibits a temperature somewhat elevated; and if it be at any time excited to motion, a slight degree of heat is manifested. The pupa appears to follow variations in atmospheric temperature, more rapidly than the larva; and as an elevation of temperature becomes necessary towards the epoch when the final metamorphosis is to take place, means are provided for it. In the Lepidoptera, the Chrysalis has itself the power of generating heat, at the period when its energies are aroused, and it is about to burst forth from its silky envelope; whilst in the Hymenoptera, it is most curious to observe an artificial warmth communicated to the pupæ, by an increased evolution of heat from the bodies of the perfect insects which crowd over their cells (§ 447).

446. The increase in the power of generating heat which is characteristic of the *Imago* or perfect Insect, is not manifested immediately on its emersion from the pupa-state; in fact at that period, when the body is soft and delicate, and the unexpanded wings hang uselessly from its sides, it parts with its heat with great rapidity. It is not until its active respiratory movements have commenced, and the whole system has been stimulated by the exercise of its locomotive powers, that the evolution of heat takes place to any remarkable extent; and whether these processes be delayed or hastened by the influence of external circumstances, the elevation of the temperature of the individual is still proportional to them. Thus, a specimen of the *Sphinx ligustri* which had only left the pupa-state about an hour and a quarter, had a temperature of about 4° above the atmosphere; whilst, at the expiration of two hours and a quarter, when it had become strong and had just taken its first flight, it had a temperature of 5·2°; and another specimen, which had been longer exerting itself in rapid flight, was as much as 9° warmer than the surrounding air. In the states of abstinence, inactivity, sleep, and hybernation, the evolution of heat is checked; and the temperature of the perfect insect may fall very nearly to that of the atmosphere. By inordinate excitement, on the other hand, a very rapid evolution of heat may be produced. Thus, a single individual of *Bombus terrestris* (Humble-bee) enclosed in a phial of the capacity of three cubic inches, had its temperature gradually raised, by violent excitement, from that of rest (2° or 3° above that of the atmosphere) to 9° above that of the external air, and had communicated to the air within the phial as much as 4° of heat within five minutes. In an experiment upon another species, *Bombus Jonella*, the temperature of the air within the phial was raised by the motion of the insect, during six or eight minutes, as much as 5·8° above that of the atmosphere; but when the bulb was held near enough to the insect to touch the tips of its wings, the mercury sunk 2·2°. This observation, which was repeated several times with the same results, shows that the vibration of the wings tends to cool the body of the insect during its flight.—In regard to the relative amount of heat evolved by different tribes of perfect Insects, Mr. Newport has ascertained that the volant insects in their perfect state have the highest temperature, while those

species which have the lowest temperature are located on the earth. Among the volant insects, those *Hymenopterous* and *Lepidopterous* species have the highest temperature, which pass nearly the whole of the daytime on the wing; of these the Hive-bee, with its long train of near and distant affinities, and the elegant and sportive Butterflies, have the highest. Next to these are probably their predatory enemies, the Hornets and Wasps, and others of the same order; and lastly, the Ants, the temperature of whose dwelling has been found to be considerably above that of the atmosphere. Next below the Diurnal insects, are the Crepuscular, the highest of which are the Sphinges and Moths, and almost equal with them are the Chaffers. In some of the *Coleoptera* (Beetle tribe) the animal heat is found to approach very nearly to that in Hymenoptera; in both of these tribes the organs of respiration are of large extent, and the quantity and activity of aeration considerable. On the other hand, the inferiority of the temperature of crepuscular Insects to that of diurnal species of the same orders, is associated with a lower degree of respiration. Nearly all the Hymenoptera are diurnal, and bear the privation of atmospheric air with greater difficulty than many other tribes. Further it would appear that some of the volant Coleoptera have, even in a quiescent state, a higher temperatnre than some of the terrestrial Coleoptera in a state of moderate activity, the difference being much increased in the active condition of the former.

447. It is among the Insects which live in societies, however (nearly all of them belonging to the order of *Hymenoptera*), that the greatest evolution of heat is manifested. Mr. Newport's observations were made principally upon the *Bombus terrestris* (Humble-bee) and *Apis mellifica* (Hive-bee).—A single individual of the former species has frequently, when moderately excited, a temperature 9° above that of the atmosphere; but that of the nest, examined in its natural situation, was from 14° to 16° above that of the atmosphere, and from 17° to 19° above that of the chalk-bank in which it was formed. But the generation of heat is increased to a most extraordinary degree, at the period when the last change is about to take place in the inclosed pupæ, which require an elevated temperature for the completion of their developmental processes. This is furnished by the individuals denominated by Huber *Nurse-bees*, of which Mr. Newport gives the following interesting account:—"These individuals are chiefly young female bees; and, at the period of hatching of nymphs, they seem to be occupied almost solely in increasing the heat of the nest, and communicating warmth to the cells by crowding upon them and clinging to them very closely, during which time they respire very rapidly, and evidently are much excited. These bees begin to crowd upon the cells of the nymphs, about ten or twelve hours before the nymph makes its appearance as a perfect bee. The incubation during this period is very assiduously persevered-in by the nurse-bee, who scarcely leaves the cell for a single minute; when one bee has left, another in general takes its place: previously to this period, the incubation on the cell is performed only occasionally, but becomes more constantly attended to nearer the hour of the development. The manner in which the nurse-bee performs its office, is by fixing itself upon the cell of the nymph, and beginning to respire very gradually; in a short time its respiration becomes more and more frequent, until it sometimes respires at the rate of

130 or 140 per minute." In one instance, the thermometer introduced among seven nursing-bees stood at 92½°, whilst the temperature of the external air was but 70°. The greatest amount of heat is generated by the nurse-bees just before the young bees are liberated from the combs, at which period they require the highest temperature. It is just after its emersion, that the young insect is most susceptible of cold; it is then exceedingly sleek, soft, and covered with moisture; it perspires profusely, and is highly sensitive of the slightest current of air. It crowds eagerly among the combs and among the other bees, and everywhere that warmth is to be obtained. It is not until after some hours, that it becomes independent of external warmth. It is interesting to remark that these bees do not incubate on cells that contain only *larvæ;* the temperature of the atmosphere of the nest being sufficiently high for the young in that condition, as well as to perfect their change into the pupa-state.—Similar observations have been made by Mr. Newport upon the temperature of the *Hive-bees;* and he has shown that the fallacy of the statements of other experimenters, as to the degree of heat maintained by them during the winter, is caused by the rapidity with which, when aroused, they can generate caloric. The temperature of individual bees in a state of moderate excitement, is usually from 10° to 15° above that of the atmosphere; but it is greatly increased about the swarming season, when incubation of the pupæ is going-on, and also when clusters are formed round the entrance of the hive. At such times Mr. N. has seen the thermometer raised as high as 96° or 98°, when the range of atmospheric temperature was only between 56° and 58°. The *mean* temperature of a hive during May was 90°, that of the atmosphere being 60°; whilst in September, the mean of the atmosphere being also 60°, that of the hive was only 66½°. During the winter, it appears that bees, like other insects, exist in a state of hybernation; though their torpidity is never so profound, as to prevent their being aroused by moderate excitement. The temperature of the hive is usually from 5° to 20° above that of the atmosphere; but it is sometimes depressed even below the freezing point. It is when artificially excited in a low temperature, that their power of generating calorie becomes most evident. Mr. N. mentions one instance in which the temperature of a hive, of which the inmates were aroused by tapping on its exterior, was raised to 102°; whilst a thermometer in the air stood at 34½°, and the temperature of a similar hive which had not been disturbed was only 48½°.

448. In regard to the degree of Heat which Insects are capable of generating, therefore, it appears that they may be ranked between 'cold-' and 'warm-blooded' animals. Like the former, they are much influenced by external temperature; although the higher species are, when in a state of moderate exercise, relatively warmer than the least cold-blooded among the Reptiles. The degree of heat they are *occasionally* capable of evolving, is nearly equal to that generated by Mammalia; but this is only required for the performance of particular functions, and, if constantly maintained in Insects, would have occasioned an unnecessary activity in the processes on which it is immediately dependent, and, by consequence, in the whole of the nutritive system. In Birds and Mammalia, however,—where, from the high development of the animal powers, the *constant* maintenance of an elevated temperature is necessary,—all

the functions are adapted to its support; and in them we no longer find any dependence upon the state of the external medium, the calorific and frigorific processes being so delicately adjusted, as to render the heat of the system extremely uniform.

449. The temperature of *Birds* is, almost without exception, higher than that of the Mammalia, varying from 100° to 111¼°. The first is that of the *Gull*, the last that of the *Swallow*. In general, the same statement may be applied to Birds, as has been made with respect to Insects,—that the temperature is greater in the species of most rapid and powerful flight, and less in those which principally inhabit the earth, as the Fowl tribe; but we find the lowest temperature of the class in the aquatic birds (which most closely approximate Reptiles in their general organisation), notwithstanding that they possess, in the thick and soft down with which they are clothed, and which is rendered impervious to fluid by the oily secretion applied with the bill, a special provision for retaining that heat within their bodies, which would otherwise be too rapidly conducted-away. It is to be remembered that, from the comparatively small size of most of the members of this class, and the larger surface which they consequently expose in proportion to their bulk, the cooling action of the surrounding medium will have a greater relative effect upon them, than upon larger animals; and the amount of heat they must generate to maintain the same internal temperature, will be greater. —The embryo of Birds requires for its development a heat nearly equal to that of the body of the parent; and this is afforded by the process of *incubation*. The contents of the egg, when lying under the body of its parent, are so situated, that the germ-spot (§ 529) is brought into closest proximity with the source of warmth. Eggs may, however, be artificially incubated,—a practice which is carried to a great extent in Egypt; and in tropical climates the heat of the sun is in some instances sufficient. Thus, the Ostrich is said to leave her eggs to be hatched by the sun's rays alone, when she breeds in the neighbourhood of the Equator; and to sit upon them, if inhabiting a more variable climate. It was observed by Mr. Knight, that a fly-catcher, which built for several successive years in one of his stoves, quitted its eggs whenever the thermometer was above 71° or 72°, and resumed her place upon the nest when the thermometer sunk again. The young of many kinds of Birds are deficient, for some time after their emergence from the egg, in the power of maintaining an independent temperature. Thus, Dr. Edwards found that young Sparrows, a week after they are hatched, have, while in the nest, a temperature of from 95° to 97°; but when they are taken from the nest, their temperature falls in one hour to 66½°, the temperature of the atmosphere being at the same time 62½°; and this rapid cooling was shown by parallel experiments not to be owing to the want of feathers. This fact, however, is not common to all Birds.

450. The temperature of *Mammalia* seems usually to range from about 96° to 104°; but more accurate observations are still required for the sake of comparison. It is remarkable that a still higher point should be attained by the animals inhabiting the coldest regions; the Arctic Fox having been found by Capt. Lyon to possess a temperature of nearly 107°, when that of the atmosphere was 14°. That of the *Cetacea* (Whale tribe) does not seem to be inferior to that of other orders;

and, to retain it within the body, the skin is enormously thickened and penetrated with oil (so as to form the substance known as *blubber*), by which the conducting power of the medium they inhabit is prevented from operating too energetically and injuriously. As far as is yet known, the temperature of the *Cheiroptera* (Bat tribe) seems more variable than that of any other order; for it has been found by Mr. Paget[*] that the amount of heat evolved by a Noctule under his observation, varied (like that of Insects) with its degree of activity, its body being but a few degrees warmer than the atmosphere after a period of prolonged repose, but its temperature rising to 99° when it had been making active exertions. The heat of different parts of the body varies a good deal according to the degree of surface exposed; and it seems greater among the viscera, than in any situation ever exposed to the air. Thus the temperature of the Human body is usually stated at 98° or 99°, from the height of thermometers placed in the mouth, axilla, &c.; but that of the stomach, according to Dr. Beaumont, is generally 100°; and that of the blood from $100\frac{1}{2}^\circ$ to $101\frac{1}{2}^\circ$.—In the young Mammalia, also, there is usually a considerable deficiency of calorifying power; but the degree of this varies considerably in the different orders of the class.

451. There is a certain group of Mammals, chiefly belonging to the orders *Rodentia* and *Cheiroptera*, which presents a marked peculiarity in regard to the generation of heat; their power of evolving it being periodically diminished, so that the temperature of their bodies falls with that of the air around, even almost down to the freezing-point; and their vital activity being lowered in the same proportion, so as to be almost entirely suspended. Yet this reduction is not attended (as in warm-blooded animals generally) with the destruction of the vital properties of their tissues; for when the temperature of their bodies is again raised by external warmth, the usual activity returns. This state, which is termed *Hybernation*, appears to be as natural to certain Mammals, as sleep is to all; and is obviously related very closely to ordinary sleep, of which state its least complete form seems but an intensification. Like many Insects, hybernating Mammals still preserve a certain *capability* of evolving heat, when a stimulus of any kind excites the animal functions, and gives a temporary activity to those of organic life. This effect may be produced by mechanical irritation, which arouses the animal from its torpidity, and accelerates its respiratory movements. Extreme cold will produce the same effect; but it does not last long; and a more profound torpidity then comes-on, which speedily ends in death, if the cold continue.—Hybernating animals, however, are by no means the only ones which exhibit a *periodical* change in the power of generating heat. It appears probable that all species of animals inhabiting climates in which the seasons are subject to much variation, vary in this respect at different parts of the year. Their power of evolving heat is greatest in the winter; so that, if exposed to severe cold during summer, their bodies are speedily cooled. The change in the colour of the fur, from dark to white, which many animals exhibit at the approach of winter, has the evident purpose (besides other objects) of diminishing the radiation of heat from its surface. That this change is occasioned by the cold

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[*] "Lectures on Surgical Pathology," Vol. I., p. 301.

of the air around, has been proved by an experiment of Capt. Ross upon a Lemming, which he had kept in his cabin until Feb. 1, and which retained its summer fur. It was then exposed on the deck to a temperature of 30° below zero; and on the following day the whitening of the fur commenced on the cheeks and shoulders, from which it gradually extended itself over the body. The Common Stoat of this country turns completely white in Scotland and the North of Continental Europe (whence it is obtained as the Ermine); in the North of England this change is occasional only; and in the midland and southern counties it is of rare occurrence. It is interesting to perceive the depressing cause thus counteracting itself, by means of that provision in the structure of the animal, which occasions the change of the colour of its fur.

452. We have now to enquire what are the *conditions* of the evolution of Heat in the animal economy. That many of the nutritive processes are subservient to it, can scarcely be doubted; but it seems peculiarly to depend upon those changes in which the function of Respiration is concerned—viz. the union of Oxygen derived from the atmosphere, with compounds of Hydrogen and Carbon existing in the living system. Wherever the aeration of the blood is extensively and actively carried-on, there is a proportionate elevation of temperature. And, on the other hand, wherever the respiration is naturally feeble, or the aeration of the blood is checked by disease or accidental obstruction, the temperature of the body falls. Thus, in spasmodic Asthma, the temperature of the Human body during a paroxysm has been found as low as 82°; in the Asiatic Cholera, a thermometer placed in the mouth has indicated but 77°; and in *Cyanosis* (or 'blue disease,' arising from malformation of the heart impeding perfect arterialisation, § 262), the same low temperature has been observed. Again, whenever the temperature of an animal is, by any extraordinary stimulus, quickly raised above that which it was previously maintaining, it is always in connection with increased activity of the respiratory movements, and increased consumption of oxygen. Thus, during the incubation of Bees, the insect, by accelerating its respiration, causes the evolution of heat and the consumption of oxygen to take place at least *twenty* times as rapidly as when in a state of repose.—Now it has been seen that arterial blood contains a larger proportion of oxygen than exists in venous blood; whilst, on the other hand, the latter contains a larger proportion of carbonic acid than exists in the former (§ 318); and it seems obvious, therefore, that during the passage of blood through the capillaries, a part of its oxygen has been exchanged for carbonic acid. The source of this product is evidently the union of atmospheric Oxygen with Carbon, furnished by disintegration of the tissues, or (more directly) by the elements of the food (§ 116); and by this union, caloric must be generated, precisely as by the more rapid union of the same materials in the ordinary process of combustion. Further, since these materials yield Hydrogen as well as carbon, and since more oxygen almost always disappears from the air which has been respired, than is contained in its carbonic acid (§ 319), it seems probable, (although this cannot be demonstrated) that this element also is subjected to the combustive process, with a further generation of caloric; and that, of the water which is exhaled from the lungs, a part has been thus produced. Further, there can be no doubt that other combustive

processes take place in the system, although these may be the chief; for example, of the Sulphur and Phosphorus which the albuminous components of the food contain, the greater proportion is thrown-off by the urinary excretion (§ 389, VII.) in the condition of sulphuric and phosphoric acids, having been combined with oxygen in the system. When all these actions are taken into account,—when the amount of heat that should be generated by the production of the quantity of carbonic acid found in the air expired during a given time, is carefully estimated, and the oxygen which has disappeared is considered as having been similarly employed in other combustive processes, especially in the formation of water,—it is found that the total so closely corresponds with the amount of heat *actually* generated by the animal during the same time, that it can scarcely be doubted that this process is the main source of calorification.*

453. Notwithstanding, however, that the Chemical theory of Animal Heat may be considered as accounting for the ordinary maintenance of a fixed temperature in the body at large, yet there are some 'residual phenomena' to which it scarcely appears applicable. Of this kind are the sudden elevation of temperature that occurs under the influence of nervous excitement, which may be either general or local; the equally sudden diminution which marks the influence of the depressing passions; and the rapid cooling of bodies in which the nervous centres have been destroyed, notwithstanding that the respiration is artificially maintained, and the circulation continues. So, again, when the spinal cord of a warm-blooded animal is divided, there is a temporary elevation of temperature in the lower extremities; but this soon subsides, and the temperature of the paralysed parts then remains permanently below the natural standard. This last fact, which corresponds with the constant deficiency of warmth observable in paralysed limbs in the Human subject, may be explained by attributing the imperfect calorification of the part to the torpor of the nutrient operations, consequent upon the deficiency of nervous energy and the want of functional activity. But this will scarcely apply to the cases first cited; and it seems not unreasonable to regard them as indications of the direct conversion of Nervous Power into Heat, of which we have strong evidence in regard to Light and Electricity.†

4. *Evolution of Electricity.*

454. Electricity is a force which may be made to act through any form of matter, and which may be produced by any other of the Physical Forces, acting under certain conditions. Thus *Motion* will generate Electricity, as in the ordinary mode of obtaining it by the friction of two dissimilar substances; and it is scarcely possible for such friction to occur, without some degree of electric disturbance. So, *Heat* will gene-

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* From the experiments of Dulong and Despretz it appeared that the whole amount of caloric generated by an animal in a given time could not thus be accounted-for; but it has been more recently shown by Prof. Liebig, that the discrepancy nearly vanishes, when the calculation is based on the more correct data since determined, as to the amount of caloric generated in the combustion of carbon and hydrogen.

† For a fuller discussion of this part of the subject, see the Author's "Human Physiology," (4th Edit.) §§ 662, 663; and "Brit. and For. Med.-Chir. Rev.," Vol. X., pp. 139, *et seq.*

rate Electricity, when applied to two dissimilar metals in contact; and the electric equilibrium is disturbed, even when two parts of the same bar are unequally heated. *Magnetism*, again, may be made to develope Electricity; as in the action of the ordinary Magneto-Electric machine. But the most frequent and powerful source of Electric disturbance, is *Chemical Action;* there being probably no instance of chemical union or decomposition, in which the electric condition of the bodies is not altered, although it may not be always easy to demonstrate the change. And, by means of the chemical actions which it produces, *Light* also may become the generator of the Electric force.—Now as many of these forces are operating in the living body, under circumstances which would appear to be peculiarly favourable to the excitement of Electricity, there can be no difficulty in accounting for its production in the organic processes of Nutrition and Secretion; and the wonder perhaps is, that the manifestations of it should be ordinarily so trivial. Thus, when the change of form of a body from solid to liquid, or from liquid to gaseous, is attended with the least chemical decomposition (as when water containing a small quantity of saline matter in solution is caused to evaporate and to leave it behind), a very decided electric disturbance is produced; and if it were not for the provisions which everywhere exist for the neutralization of the effects of such actions, by the conducting power of the parts in which they occur and of the bodies around them, such electric disturbances could scarcely fail to exert an important influence on the organic functions.

455. *Electricity in Vegetables.*—That the ordinary processes of Vegetable growth are attended with a disturbance of electric equilibrium, which is manifested when the bodies in which it takes place are effectually insulated, seems to have been proved by the experiments of Pouillet. Several pots filled with earth, and containing different seeds, were placed on an insulated stand in a chamber, the air of which was kept dry by quick-lime; and the stand was placed in connection with a condensing electrometer. During germination, no electric disturbance was manifested: but the seeds had scarcely sprouted, when signs of it were evident; and when the young plants were in a complete state of growth, they separated the gold leaves of the electrometer half an inch from each other. It was calculated by him that a vegetating surface of 100 square metres in extent produces in a day more electricity than would be sufficient to charge the strongest battery; and he not unreasonably considered that the growth of plants may be one of the most constant and powerful sources of atmospheric electricity. The disengagement of vapour from the surface of the leaves would alone be sufficient to produce such a disturbance, as the fluid from which it is given-off is always charged with saline and other ingredients; and the gaseous changes which are effected by the leaves, upon the oxygen and carbonic acid of the atmosphere, may be regarded as additional sources of its development. During the various processes of decomposition and recomposition which take place in the assimilation of the Vegetable juices, we should expect that electric equilibrium would be sometimes disturbed, sometimes restored. Of this, the following facts, amongst others, appear to be sufficient evidence. If a wire be placed in apposition with the bark of a growing plant, and another be passed into the pith, contrary electrical states are indicated, when they are applied to

an electrometer. If platinum wires be passed into the two extremities of a fruit, they also will be found to present opposite conditions. In some fruits, as the apple or pear, the stalk is negative, the eye positive; whilst in such as the peach or apricot, a contrary state exists. If a prune be divided equatorially, and the juice be squeezed from its two halves into separate vessels, its portions will in like manner indicate opposite electrical states, although no difference can be perceived in their chemical qualities.*

456. *Electricity in Animals.*—All that has been said of the effects of vegetation in producing a disturbance of Electric equilibrium, will manifestly apply to the nutritive processes of Animals also; and there is no deficiency of indications that such is the case. Thus, Donné found that the skin and most of the internal membranes are in opposite electrical states; and Matteucci has seen a deviation of the needle amounting to 15° or 20°, when the liver and stomach of a rabbit were connected with the platinum ends of the wires of a delicate galvanometer. It may be questioned whether the differences in the secretions of these parts were the causes or the effects of their electric conditions. According to Matteucci, it could not be by their chemical action on the wires that the manifestation was produced, since it became very feeble or entirely ceased on the death of the animal. The more recent experiments of Mr. Baxter,† which were directed to the determination of the relative electrical condition of secreting surfaces, and of the blood in the veins returning from them, seem to confirm the belief that an electric disturbance takes place in the very act of secretion. He found that when one of the electrodes was placed on the intestinal surface, and the other inserted into the branch of the mesenteric vein proceeding from it, a deflection of the needle to the extent of 4° or 5° was produced, indicating a positive condition of the blood; no effect, on the other hand, was produced, when the second electrode was inserted into the artery of the part. These effects cease soon after the death of the animal, which is not the case with those which proceed from simple chemical differences between the blood and the secreted product.‡—The researches of M. du Bois-Reymond, taken in connection with the preceding, have now made it apparent that there are no two parts of the body, save those which correspond on opposite sides,§ whose electric condition is precisely the same; and that the differences between them are greater, in proportion to the diversity of the vital pro-

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* "Annales de Chimie," Tom. LVII.

† "Philosophical Transactions," 1848, p. 243.

‡ These experiments may seem confirmatory of the theory respecting Secretion proposed by Dr. Wollaston; who, observing the connection between electricity and chemical action, was led to think that all the secretions in the body are the effect of electrical agency acting in various modes, and that the qualities of each secretion point-out what species of electricity preponderated in the organ which forms it;—the existence of free acid in the urine and gastric juice, and of free alkali in the bile and saliva, marking the prevalence of positive electricity in the kidneys and stomach, whilst an excess of negative electricity is indicated in the liver and salivary glands. But it is more likely that the disturbance of Electricity is the *result* of chemical changes, whose source is the Vital force, than that it is itself the cause of those changes.

§ A wonderfully-minute difference in the respective conditions of these, is sufficient to produce a very decided effect upon a delicate galvanometer; thus in the performance of M. du Bois-Reymond's experiment (§ 458), it is found that the slightest abrasion of the skin of one of the immersed fingers produces a considerable deflection in the needle.

cesses which are taking-place in them, and to the activity with which these are carried-on.

457. The influence of active molecular changes in producing Electric disturbance, is peculiarly well seen in the case of Muscles and Nerves; whose substance undergoes more rapid changes, alike of disintegration and of nutritive reparation, than does that of any other tissues in the body.—It has been shown by Matteucci,* that if an incision be made into a Muscle of a living animal, and the nerve of a 'galvanoscopic frog'† be introduced into the wound, in such a manner that its extremity is applied to the deepest part, and another portion to the lips or to the surface of the muscle, the leg of the frog is thrown into contraction; thus proving that a difference exists in the electric condition of the deeper and the more superficial parts of the animal. This phenomenon is exhibited even when the muscle is separated from the body; but when the experiment is many times repeated, the contractions are observed to become feebler and feebler, and at last to cease altogether, their duration being greater when a muscle of a cold-blooded animal, than when that of a warm-blooded animal is employed. A galvanic pile may even be formed of pieces of fresh muscle, provided they be so arranged that the internal substance of each is in contact with the external surface of the next; and thus it may be shown, by the galvanometer, that a current is continually proceeding from the interior to the surface of every muscle. This current exists when the muscle is in a completely passive state; and its intensity seems then to depend upon the activity of the nutrient changes taking place in it. Its phenomena have been carefully investigated by M. du Bois-Reymond, who has arrived at the general conclusion, that "when any point of the longitudinal section of a muscle is connected by a conductor with any point of its transverse section, an electric current is established, which is directed, in the muscle, from its longitudinal to its transverse section."‡ The most powerful influence on the galvanometer is produced, when a portion of the outer surface (or natural longitudinal section) of a muscle is laid upon one of the electrodes, and a portion of its internal part exposed by cutting it across (or artificial transverse section) is placed against

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* "Lectures upon the Physical Phenomena of Living Beings;" LECT IX.

† The 'galvanoscopic frog,' which has been continually employed by Prof. Matteucci to test minute electric disturbances which are scarcely appreciable by a galvanometer, is simply the leg of a recently-killed frog, with the crural nerve, dissected out of the body, remaining in connection with it; the leg being enclosed in a glass tube covered with an insulating varnish, and the nerve being allowed to hang freely from its open end, when two points of the nerve are brought in contact with any two substances in a different electrical state, the muscles which it supplies are thrown into contraction.

‡ See Dr. Bence Jones's "Abstract of the Discoveries in Animal Electricity by M. Emil du Bois-Reymond," p. 90.—For the precise comprehension of the above law, it is requisite that the terms of its enunciation should be fully understood. The entire muscle being composed of a mass of fibres having a generally-parallel direction, and attached at their extremities to tendinous structure (which has in itself little or no electro-motor power, but is a conductor of electricity), it follows that the tendon or tendinous portion of a muscle represents a surface formed by the *bases* of the muscular fibres considered as prisms, which may be designated as its *natural transverse section*. On the other hand, the fleshy surface of the muscle, which is formed only by the *sides* of the fibres considered as prisms, may be regarded as the *natural longitudinal section* of the muscle. Again, if a muscle be divided in a direction more or less perpendicular to its fibres, an *artificial transverse section* will be made; whilst, if the muscle be torn lengthways in the direction of its fibres, an *artificial longitudinal section* will be made.

the other. The same results may be obtained, not merely with the entire muscle, but with insulated portions of it, and even with a single primitive fasciculus; so that every integral particle of the muscular substance must be an independent centre of electro-motor action.

458. The existence of an Electrical current in the Frog, passing during its whole life from its extremities towards its head, has been known since Nobili applied the galvanometer to the elucidation of the phenomena first observed by Galvani; but it was at first supposed to be peculiar to this animal. Even Matteucci, for some time after his discovery of the 'muscular current,' regarded the 'proper current of the frog' as something essentially different. More recently, however, it has been shown that the latter is but a special case of the former, being dependent upon the particular arrangement of the muscles and tendons in the limbs and body of this animal. The community of origin of the 'muscular current' and of the 'proper current of the frog,' is further indicated by the circumstance that they are both modified in the same manner by agents which affect the vitality of the muscle; and it is particularly remarkable that poisoning with sulphuretted hydrogen should almost immediately put an end to both, although narcotic poisons have very little influence. The 'proper current of the frog' bears this curious analogy to the electric discharges of Fishes presently to be described;—that it is not manifested if the connection be made between corresponding points of the opposite sides; but that it shows itself when the communication is made between points higher or lower in the body, whether on the same or opposite sides.

459. That a change in the electric state of Muscles takes place in the act of contraction, had been ascertained by the experiments of Prof. Matteucci; but as he was only able to detect this by the 'galvanoscopic frog' (the galvanometer he employed not giving unquestionable indications of it), he was not able to determine its nature with accuracy. This determination has been accomplished, however, by M. du Bois-Reymond; who has shown that (contrary to the belief of Matteucci) the contraction of a muscle is attended with *a marked diminution of its electro-motive power*, the muscular current being diminished, or even reduced to zero. This alteration has been demonstrated by M. du Bois-Reymond in the living animal, after the following manner. The two feet of a live Frog were immersed in the two connecting vessels, but one of the legs was paralysed by division of its sciatic plexus; the muscular currents of the muscles of the two limbs neutralised each other, so long as they remained at rest; but upon the frog being poisoned with strychnia, so that tetanic convulsions occurred in one limb, whilst the other remained motionless, the current in the former limb was weakened, whilst that of the latter remained unaffected, and a deflection of the needle took place, indicating an upward current in the paralysed limb, and a downward current in the tetanized one. The same thing may be shown in the Human subject, by dipping the fore-fingers of the two hands into the two conducting vessels connected with the galvanometer, so that the two arms are included in opposite directions in the circuit; when if, after the needle (which usually undergoes a temporary disturbance on their first immersion) has come to a state of rest, all the muscles of one of the arms be strongly and permanently contracted, so as to give them the greatest possible tension without changing the

position of the arm, the needle is instantly deflected, always indicating a current from the hand to the shoulder, that is, an *upward* current in the contracted arm. This change, however, is so extremely slight, that a very delicate galvanometer is requisite to render it perceptible. Its intensity depends very much on the muscular energy of the experimenter; and even the greater power which the right arm usually possesses, becomes perceptible in the greater deflection of the needle when *it* is put in action.*

460. The discovery that an electric current exists in Nerves, the conditions of which are in most respects similar to that of the muscular current, is entirely due to M. du Bois-Reymond. When a small piece of a nerve-trunk is cut-out from the recently-killed body, and is so placed upon the electrodes that it touches one of them with its surface (or natural *longitudinal* section), and the other with its cut extremity (or artificial *transverse* section), a considerable deflection of the index is produced, the direction of which always indicates the passage of a current from the interior to the exterior of the nerve-trunk. It is indifferent in regard to the direction of the current, whether the central or the peripheral cut extremity be applied to the electrode; and in fact, the most powerful effect is obtained by doubling the nerve in the middle, and applying both transverse sections to one electrode, whilst the loop is applied to the other. On the other hand, if the two cut extremities be applied to the two electrodes respectively, no decided effect is produced; and the same neutrality exists between any two points of the surface of the trunk, equidistant from the middle of its length; but if the points be not equidistant, then a slight deflection is produced, indicating that the parts nearer the middle are positive to those nearer the extremities. It has not been found possible, owing to the small size of the nerve-trunks experimented-on, to test in a similar manner the relative state of different points of their transverse section; but there can be little doubt, from the complete conformity which exists in other respects between the nervous and muscular currents, that the same law would be found to prevail in this as in the former case; namely, that the points nearer the surface are positive to those nearer the centre. There is no difference between the motor and the sensory nerves in regard to the direction of this current, the existence of which, like that of the muscular, must be considered as derived from the electromotive action of the molecules of the nerve.—Now the state of activity which is induced in a nerve-trunk by passing an electric current through a portion of it, is easily proved to be, not the direct consequence of the electric force, but the result of the excitement of the *proper force of the nerve* by the agency of Electricity. Thus, as Prof. Matteucci has shown, when an electric current is transmitted through the muscles of the thighs of a living animal, the positive pole

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* Of this very remarkable experiment, which was first made by M. du Bois-Reymond, the Author has himself (through that gentleman's kindness) been a witness; and he gladly bears his testimony to its highly satisfactory character. The success of M. du Bois-Reymond in these and similar investigations, is doubtless due in great part to the marvellous sensitiveness of the galvanometer he employs, the coils of which consist of *three miles* of wire, as well as to the perfection of the various arrangements by which he is enabled to avoid or eliminate sources of error; but it must be attributed in great part also to the philosophic method on which his inquiries are planned, and to the skill and perseverance with which they are carried-out.

being placed above and the negative pole below, so that the current passes in the direction of the efferent or motor nerves, there is not only a strong *contraction* of the muscle traversed, but also of the muscles of the leg below; indicating that an influence is transmitted through the nerves which proceed to them. On the other hand, when the current is transmitted in the inverse direction, the positive pole being below, so that it is directed along the course of the afferent nerves, or towards the nervous centres, *pain* is produced, without any muscular contraction save in the muscle traversed; showing that the influence is now transmitted towards the nervous centres.* Again, it has been clearly established by other experiments, that an electric current traversing a muscle, never quits its substance to travel along the filaments of the nerves distributed through it; so that it is obvious that the influence which in the one case excites muscular contraction, and in the other case occasions pain, is not Electricity, but Nervous Force generated by the passage of the electric current through the muscle, in the nerves which are distributed to it. —When an 'electrotonic' state is thus induced in a nerve, by the agency of a continued electric current transmitted through a part of its trunk, it is found that the 'nervous current' just described is *increased* if the electric current have the *same* direction as that between the transverse and longitudinal sections of the nerve, and is *diminished* if its direction be *contrary*. When, on the other hand, a nerve is 'tetanized' by passing an interrupted and alternating current through a portion of it, the effect is, as in the case of muscle, to produce a diminution, or even a complete suspension, of its own proper current. A similar diminution, or even a reversal of the current, has been found by M. du Bois-Reymond to follow severe injuries of the nerve, by mechanical, chemical, or thermal agencies.

461. There are certain animals which possess the power of accumulating Electric force within their bodies, and of discharging it at-will in a violent form; and with the exception of some Insects and Mollusca, which have been said (though this is doubtful) to communicate sensible shocks, these animals are all included in the class of *Fishes*. Above seven species of this class, belonging to five genera, are known to possess electric properties; and it is curious that these genera belong to tribes very dissimilar from one another, and that, though each has a limited geographical range, one species or other is found in almost every part of the world. Thus, the three species of *Torpedo*, belonging to the Ray tribe, are found on most of the coasts of the Atlantic and Mediterranean, and sometimes so abundantly as to be a staple article of food. The *Gymnotus*, or electric Eel, is confined to the rivers of South America. The *Silurus* (more correctly the Malapterurus), which approaches more nearly to the Salmon tribe, occurs in the Niger, the Senegal, and the Nile. The *Trichiurus*,† or Indian Sword-fish, is an inhabitant of the Indian Seas. And the *Tetraodon* (one of a genus allied to the Diodon or globe-fish) has only been met-with on the coral banks of Johana, one of the Comoro Islands.—These Fishes have not all been examined with the same degree of attention; but it seems probable that the phenomena which they exhibit, and the structural

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* "Philosophical Transactions," 1850, p. 295.

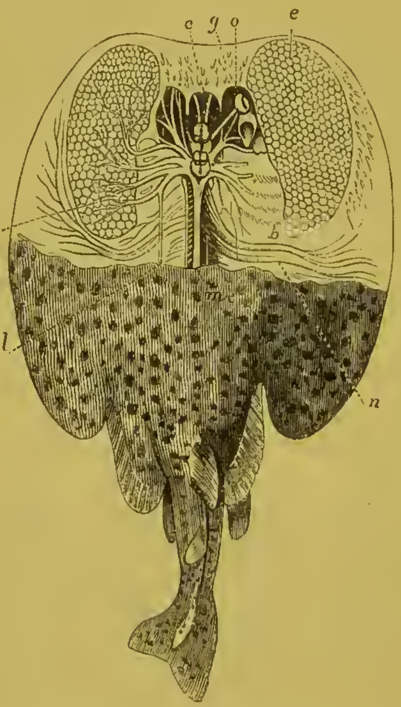
† There is some doubt, however, as to the real character of the fish to which this name has been given.

peculiarities with which these are connected, are essentially the same throughout. The peculiar characteristic of all is the power of giving, to any living body which touches them, a shock resembling in its effects that produced by the discharge of a Leyden jar. This is of very variable intensity in different species and individuals, and at different times. The *Gymnotus* will attack and paralyse horses, as well as kill small animals; and the discharges of large fish (which are 20 feet long) sometimes prove sufficient to deprive men of sense and motion. The effects of the contact of the *Torpedo* are less severe and soon pass off; but the shock is attended with considerable pain when the fish is vigorous. The electrical organs appear to be charged and discharged to a certain extent at the will of the animals. Their power is generally exerted by the approach of some other animal, or by some external irritation; but it is not always possible to call it into action, even in vigorous individuals. It usually diminishes with the general feebleness of the system, though sometimes a dying fish exerts considerable power. All electrical fishes have their energy exhausted by a continual series of discharges; hence it is a common practice with convoys in South America, to collect a number of wild horses and drive them into the rivers, in order to save themselves, when they pass, from being injured by the fish. If excessively exhausted, the animals may even die; but they usually recover their electrical energy after a few hours' rest.

462. The *Torpedo*, from its proximity to European shores, has been most frequently made the subject of observation and experiment; and the following are the most important results of the investigations which have been made upon it by various enquirers.—That the shock perceived by the organs of sensation in Man is really the result of an Electric discharge, has now been fully established. Although no one has ever seen a spark emitted from the body of one of the fish, it may be easily made manifest, by causing the Torpedo or Gymnotus to send its discharge through a slightly-interrupted circuit. The galvanometer is influenced by the discharge of the Torpedo, and chemical decomposition may be effected by it, as well as magnetic properties communicated to needles. It seems essential to the proper reception of the shock, that two parts of the body should be touched at the same time, and that these two should be in different electrical states. The most energetic discharge is procured from the Torpedo, by touching the back and belly simultaneously, the electricity of the dorsal surface being positive, and that of the ventral negative; and by this means the galvanometer may be strongly affected, every part of the back being positive with respect to every part of the opposite surface. When the two wires of the galvanometer are applied to the corresponding parts of the two sides of the same surface, no influence is manifested; but, if the two points do not correspond in situation, whether they be both on the back or both on the belly, the index of the galvanometer is made to deviate. The degree of proximity to the electric organ appears to be the source of the difference in the relative state of different parts of the body; those which are near to it being always positive in respect to those more distant. Dr. Davy found that however much Torpedos were irritated through a single point, no discharge took place; and he states that when one surface only is touched and irritated, the fish themselves appear to make an effort to bring the border of the other surface, by muscular con-

traction, into contact with the offending body; and that this is even done by fœtal fish. If a fish be placed between two plates of metal, the edges of which are in contact, no shock is perceived by the hands placed upon them, since the metal is a better conductor than the human body; but, if the plates be separated, and, while still in contact with the opposite sides of the body, the hands be applied to them, the discharge is at once rendered perceptible, and it may be passed through a line formed by the moistened hands of two or more persons, the extremities being brought into relation with the opposite plates.—The electrical phenomena of the *Gymnotus* are essentially the same with those of the Torpedo; but the opposite electrical states are found to exist, not between the dorsal and ventral surfaces, but between the head and the tail; so that the shock is most powerful, when the connection is formed between these two extreme points.

Fig. 190.



Electrical Apparatus of *Torpedo*:—*b*, branchiæ; *c*, brain; *e*, electric organ; *g*, cartilage of cranium; *m e*, spinal cord; *n*, nerves to the pectoral fins; *n l*, lateral nerves to the body; *np*, large nerves (pneumogastric) to the electric organ; *o*, eye.

463. It has been ascertained by experiment, that the manifestation of this peculiar power depends upon the integrity of the connection between the Nervous centres and certain organs peculiar to Electrical fishes. In the Torpedo the Electric organs are of flattened shape (Fig. 190, *e*), and occupy the front and sides of the body, forming two large masses, which extend backwards and outwards from each side of the head. They are composed of two layers of membrane, between which is a whitish soft pulp, divided into columns by processes of the membrane sent-off so as to form partitions like the cells of a honey-comb; the ends of these columns being directed towards the two surfaces of the body. The columns are again subdivided horizontally by more delicate partitions, which form each into a number of distinct cells; the partitions are extremely vascular, and are profusely supplied with nerves, of which the fibres seem to break up into minuter fibrillæ to form plexuses upon these membranes. The fluid contained in the electrical organs forms so large a proportion of them, that the specific gravity of the mass is only 1026, whilst that of the body in general is about 1060; and, from a chemical examination of its constituents, it seems to be little else than water, holding one-tenth part of albumen in solution, with a little chloride of sodium.—The electrical organs of the *Gymnotus* are essentially the same in structure, though differing in shape in accordance with the conformation of the animal; they occupy one-third of its whole bulk, and run along nearly its entire

length; there are, however, two distinct pairs, one much larger than the other. The prisms are here less numerous, but are much longer; for they run in the direction of the length of the body, a difference which is productive of a considerable modification of the character of the discharge (§ 465).—In the *Silurus* there is not any electrical organ so definite as those just described; but the thick layer of dense areolar tissue, which completely surrounds the body, appears to be subservient to this function; it is composed of tendinous fibres interwoven together, and of an albuminous substance contained in their interstices, so as to bear a close analogy with the cellular partitions in the special organs of the Torpedo and Gymnotus.—The organs of the other Fishes said to electrical, have not yet come under the notice of any anatomist.

464. In all these instances, the Electrical Organs are supplied with Nerves of very great size, larger than any others in the same animals, and larger than any nerve in other animals of like bulk. They all arise in the *Torpedo* from a ganglionic mass situated behind the Cerebellum, and connected with the Medulla Oblongata, to which the name of 'electric lobe' has been given; the first two of them issue from the cranium in close proximity with the 5th pair, and have been regarded as belonging to it, although their real origin is different; whilst, from the distribution of the third electrical nerve to the stomach, after sending its principal portion to the electrical organ, it would seem analogous to the 8th pair or pneumogastric (Fig. 190, *n p*).—The electrical nerves in the *Gymnotus* are believed to arise from the spinal marrow alone; while those of the *Silurus* are partly intercostals and partly belong to the 5th pair.—The integrity of the nerves is essential to the full action of the electrical organs. If all the trunks be cut on one side, the power of that organ will be destroyed, but that of the other may remain uninjured. If the nerves be partially destroyed on either or both sides, the power is retained by the portion of the organs still in connection with the centres. The same effects are produced by tying the nerves, as by cutting them. Even slices of the organ entirely separated from the body, except by a nervous fibre, may exhibit electrical properties. Discharges may be excited by irritation of the brain when the nerves are entire, or of the part of the divided trunk distributed on the organ; but on destroying the 'electric lobe' of the brain, the electric power of the animal ceases entirely, although all the other ganglionic centres may be removed without impairing it. It is remarkable, however, that after the section of the electrical nerves, Torpedos appear more lively than before the operation, and actually live longer than others, not so injured, which are excited to discharge frequently.—Poisons which act violently on the nervous system, have a striking effect upon the electrical manifestations of these fish; thus, two grains of muriate of Morphia were found by Matteucci to produce death after about ten minutes, during which time the discharges were very numerous and powerful; and Strychnia also excited powerful discharges at first, succeeded by weaker ones, the animals dying in violent convulsions. When the animals were under the influence of strychnia, it was observed that the slightest irritation occasioned discharges; a blow given to the table on which the animal was placed, being sufficient to produce this effect. If the spinal cord were divided, however, no irritation of the parts situated below the section called-forth a shock.—It has also been ascertained

by Matteucci, that the electric power is suspended when the Torpedo is plunged into water at 32°, and is recovered again when it is immersed in water of a temperature from 58° to 60°; and that this alternation may be repeated several times upon the same fish. But if the temperature be raised to 86°, the Torpedo soon ceases to live, and dies while giving a great number of violent discharges.*

465. From all these facts it seems an almost unavoidable inference, that the Electric force is developed in the electric organ, by a disturbance of its equilibrium consequent upon Nervous Agency. Such a disturbance may be conceived to take place in every one of those minute cells, into which the prism is divided by transverse partitions; the two electricities (to use the current phraseology) being separated by nervous agency, as they are in the tourmaline by heat. Now by the multiplication of such cells in each prism, a 'pile' would be produced, at the two extremes of which the greatest differences in the electric condition would be found; and the *intensity* of the discharge would thus depend upon the number of elements in the pile, while its *quantity* would be proportional to the multiplication of the separate prisms. This is precisely what holds good in nature; for the electric discharge of the Gymnotus is far more intense than that of the Torpedo, as might be expected from the multiplication of its cells; so that, according to Prof. Faraday, a single medium discharge from this animal gives a shock equal to that of a battery of fifteen Leyden jars, containing 3500 square inches, charged to its highest degree.—Further evidence that the force which enables the Electric Fishes to give sensible manifestations of Electricity, is the same as that which excites Contraction when transmitted to the Muscles, is derived from the close conformity between the conditions under which the two phenomena respectively occur. The connection of the organs specially appropriated to each of these actions, with the Nervous System, the dependence of their functions upon the integrity of this connection and upon the will of the animal, the influence of stimulation applied to the nervous centres or trunks, the effect of ligature or section of the nerve, and the results of poisonous agents, are all so remarkably analogous in the two cases, that it seems scarcely possible to refuse assent to the proposition, that the Nervous power is the agent which is instrumental in producing both sets of phenomena. Still, however, no proof whatever can be derived from this source, of the *identity* of Nervous influence with any form of Electricity; since all that can be inferred from it is, that as, by the influence of the Nervous system on one class of organs, sensible Contraction is produced, so by its influence on another class of organs, Electricity is generated. On the other hand, all the experiments of Prof. Matteucci confirm the conclusion based on other grounds, that the two forces are *not* identical, but that they are 'correlated,' each being able to generate the other.†

466. Regarding the uses of the Electrical organs to the animals possessing them, no very certain information can be given. It is doubtful to what extent their power is subservient to the prehension of food, which was once supposed to have been their principal object; since it is known

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* See Prof. Matteucci's "Lectures on the Physical Phenomena of Living Beings," p. 216.

† See the Author's Memoir 'On the Mutual Relations of the Vital and Physical Forces,' in "Philos. Transact.," 1850.

that the Gymnotus eats very few of the fishes which it kills by its discharge; and young Torpedos kept by Dr. Davy for five months ate nothing, though supplied with small fishes both dead and alive, but nevertheless increased in strength and in electrical energy. The electric power of young Torpedos is much less exhaustible than that of the adults; this is readily accounted-for by the fact of the greater energy of the vital processes in young than in old animals. Dr. D. experienced shocks from fœtal fish, which he was removing from the abdomen of the parent. He believes that the electric action may assist the function of respiration, by decomposing the water in the neighbourhood of the gills, when the animal, being buried in sand or mud, might be unable to obtain the requisite supply of oxygen in the ordinary way; but its chief use he considers to be to guard the fish from its enemies. Another function, however, may not improbably be influenced by it,—that of Digestion; and this in two ways. It is well known that the vital properties of living tissues are so completely destroyed by a violent electric discharge, that they are disposed to pass more readily than in other cases into decomposition, the incipient stage of which is favourable to digestion; the shortness of the intestinal canal of the Torpedo would seem to render some assistance of this kind peculiarly necessary. The process of digestion may also be aided by the continued action of electricity through the nerves of the stomach, which have been mentioned to be peculiarly connected in the Torpedo with those of the Electrical organs; a supposition which derives some support from the fact mentioned by Dr. Davy, that digestion appeared to be arrested in an individual which had been exhausted by frequent excitement to discharge itself: it should be kept in view, however, that the general depression of the vital powers may have been the cause of the check put to the process.* It is not impossible, as Dr. Roget has suggested, that the electrical organs may communicate to the fish perceptions of electrical states and changes in the surrounding bodies (very different from any that we can feel), in the same way as other organs of sense convey perceptions with regard to light and sound.†

CHAPTER XI.

OF GENERATION AND DEVELOPMENT.

1. *General Considerations.*

467. If the changes which Living Beings undergo during the period of their existence, and the termination of that existence by the separation of their elements at a period more or less remote from their first combination, be regarded as distinguishing them in a striking and evident

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* See Dr. J. Davy's 'Experiments and Observations on the *Torpedo*' in "Philos. Trans.," 1832, and "Researches, Physiological and Anatomical."

† For some curious instances of an unusual development of Electricity in the Human Subject, see the Author's "Human Physiology," 4th Edit., § 673.

manner from the masses of Inert Matter which surround them, still more is their difference manifested in that series of processes, which constitute the function of *Generation*. A very unnecessary degree of mystery has been spread around the exercise of this function, not only by general enquirers, but by scientific physiologists. It has been regarded as a process never to be comprehended by man, of which the nature and the laws are alike inscrutable. A fair comparison of it, however, with other functions, will show that it is not in reality less comprehensible or more recondite than any one of them;—that our acquaintance with each depends upon the facility with which it may be submitted to investigation;—and that, if properly enquired-into by an extensive survey of the animated world, the real character of the process, its conditions, and its mode of operation, may be understood as completely as those of any other vital phenomenon.

468. It may be considered as a fundamental truth of Physiological Science, that *every living organism has had its origin in a pre-existing organism.* The doctrine of 'spontaneous generation,' or the supposed origination of Organised structures, *de novo*, out of assemblages of Inorganic particles, although at different times sustained with a considerable show of argument, based on a specious array of facts, cannot now be said to have any claim whatever to be received as even a possible hypothesis; all the facts on which it claimed to rest having either been themselves disproved, or having been found satisfactorily explicable on the general principle *omne vivum ex ovo.* Thus, the appearance of Animalcules in infusions of decaying organic matter, the springing-up of Fungi in spots to which it would not have been supposed that their germs could have been conveyed, the occurrence of Entozoa in the bodies of various animals into which it seemed almost beyond possibility that their eggs could have been introduced, with other facts of a like nature, may now be accounted-for, without any violation of probability, by our increased knowledge of the mode in which these organisms are propagated. For it is now well ascertained, that the germs of Fungi and of many kinds of Animalcules are diffused through the atmosphere, and are conveyed by its movements in every direction: and if to decomposing substances, of a kind that would otherwise have been most abundantly peopled by these organisms, such air only be allowed to have access, as has been deprived of its organic germs by filtration (so to speak) through a red-hot tube or through strong sulphuric acid, no living organisms will make their appearance in them; whilst, in a few hours after the exposure of the very same substances to ordinary atmospheric air, it is found to be crowded with life.* And when it is borne in mind in the case of the Entozoa, that the members of this class are remarkable for the immense number of eggs which most of them produce, for the metamorphoses which many of them are known to undergo, and for the varieties of form under which there is reason to suspect that the same germs may develope themselves, it becomes obvious that no adequate proof has yet been afforded that they have been, in any particular case, otherwise than the products of a pre-existing living organism.—This, again, is the conclusion to which all the most general doctrines of Physiology necessarily conduct us. For it is

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* See the experiments of Schulze, in the "Edinb. New Phil. Journ." 1837, p. 165.

most certain that we know nothing of Vital Force, save as manifested through Organised structures; whilst, on the other hand, the combination of Inorganic matter into Organised structures is one of the most characteristic operations of Vital Force; hence it is scarcely conceivable that any operation of Physical Forces upon Inorganic matter should evolve a living Organism. Nor is such a conception rendered more feasible by the admission that Vital Force stands in such a relation to the Physical Forces, that we may regard the former as a manifestation of the latter, when acting through Organised structures; since according to this view also, no Vital force can be manifested, and no Organisation can take place, except through a pre-existing Organism.—(See GENERAL PHYSIOLOGY.)

469. It may be further considered as an established Physiological truth, that, when placed under circumstances favourable to its complete evolution, every germ will develope itself into the likeness of its parent; drawing into itself, and appropriating by its own assimilative and formative operations, the nutrient materials supplied to it; and repeating the entire series of phases through which its parent may have passed, however multiform these may be.* Now the germs of all tribes of Plants and Animals whatever, bear an extremely close relation to each other in their earliest condition; so that there is no appreciable distinction amongst them, which would enable it to be determined whether a particular molecule is the germ of a Conferva or of an Oak, of a Zoophyte or of a Man. But let each be placed in the conditions it requires; and a gradual evolution of the germ into a complex fabric will take place, the *more general* characters of the new organism preceding the *more special*, as already explained (§§ 73, 74). These conditions are not different in kind from those which are essential to the process of Nutrition in the adult; for they consist, on the one hand, in a due supply of Aliment in the condition in which it can be appropriated; and, on the other hand, in the operation of certain external agencies, especially Heat which seems to supply the *force* requisite for the developmental process (§ 342). Now although we may not be able to discern any such ostensible differences in the germs of different orders of living beings, as can enable us to discriminate them one from another, yet, seeing so marked a diversity in their operations under circumstances essentially the same, we cannot do otherwise than attribute to them distinct properties: and it will be convenient to adopt the phrase *germinal capacity* as a comprehensive expression of that peculiar endowment, in virtue of which each germ developes itself into a structure of its own specific type, when the requisite forces are brought to bear upon it, and the requisite materials are supplied to it.† Thus, then, every act of Development may be

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* The apparent exceptions to this rule, which have been brought together under the collective term 'Alternation of Generations,' will be presently considered, and will be shown to be only exceptional when misinterpreted (§ 478).

† This term is preferred to that of 'germ-power' suggested by Mr. Paget, because the latter seems to imply that the *force* of development exists in the germ itself. Now if this were true, not only must the whole formative power of the adult have been possessed by its first cell-germ, but the whole formative power of all the beings simultaneously belonging to any one race, must have been concentrated in the first cell-germ of their original progenitor. This seems a *reductio ad absurdum* of any such doctrine; and we are driven back on the assumption (which all observation confirms), that the *force* of development is derived from *external* agencies.

considered as due to the force supplied by *Heat* or some other physical agency, which, operating through the Organic germ, exerts itself as formative power; whilst the mode in which it takes effect is dependent upon the properties or endowments of the substances through which it acts, namely, the germ on the one hand, the alimentary materials on the other,—just as an Electric current transmitted through the different nerves of sense, produces the sensory impressions which are characteristic of each respectively; or, as the same current, transmitted through one form of Inorganic matter, produces Light and Heat, through another, Chemical change, or through another, Magnetism.

470. In the development of any living being, therefore, from its primordial germ, we have three sets of conditions to study;—namely, *first*, the physical forces which are in operation; *second*, the properties of the germ, which these forces call into activity; and *third*, the properties of the alimentary materials, which are incorporated in the organism during its development. There is evidence that each of these may have a considerable influence on the result; but in the higher organisms it would seem that the second is more dominant than it is in the lower. For among many of the lower tribes, both of Plants and Animals, there is reason to believe that the range of departure from the characters of its parent, which the organism may present, is considerably greater than that of the higher; and that this is chiefly due to the external conditions under which it has been developed. The forms of a number of species of the lower Fungi, for example, appear to be in great part dependent on the nature of their aliment (§ 26, *note*); so among the Entozoa, it is now fully established that those which were formerly distinguished as *Cystica*, are only *Cestoidea* that are prevented by the circumstances under which they exist from attaining their full development (§ 570); and the production of a fertile 'queen' or of an imperfect 'worker,' among the Hive-bees, appears to be entirely determined by the food with which the larva is supplied (§ 119). No such variations have been observed among the higher classes; in which it would seem as if the form attained by each germ is more rigidly determined by its own endowments; a modification in the other conditions, which in the lower tribes would considerably affect the result, being in them unproductive of any corresponding change. For if such modification be considerable, the organism is unable to adapt itself to it, and consequently either perishes or is imperfectly developed; whilst, if it be less potent, it produces no obvious effect. Thus, a deficiency of Food in the growing state of the higher Animal, will necessarily prevent the attainment of the full size; but it will not exert that influence on the relative development of different parts, which it does among Plants (in which it favours the production of flowers and fruit in place of leaves, § 92), or which it seems to exercise in several parallel cases among Animals (§ 118). So, again, a deficiency of Heat may slightly retard the development of the Chick; but if the egg be allowed to remain long without the requisite warmth, the embryo dies, instead of passing into a state of inactivity like that of Reptiles or Insects.

471. The extent, indeed, to which these external conditions may affect the development of the inferior organisms, must not be in the least judged-of by that to which their operation is restricted in the higher;

and it is probable that we have yet much to learn on the subject. At present, it may be stated as a problem for determination, whether, from a being of superior organization, *lower* forms of living structure, capable of maintaining an independent existence, and of propagating their kind, can ever originate, by an imperfect action of its formative powers (§ 566). Various morbid growths, such as Cancer-cells, to which the higher organisms are liable, have been looked-upon in this light: these have certainly a powerful vitality of their own, which enables them to increase and multiply at the expense of the organism which they infest; and they have also an energetic reproductive power, by which they can propagate their kind, so as to transmit the disease to other organisms, or to remote parts of the same organism: but such growths are not independent; they cannot maintain their own existence, when detached from the organism in which they are developed; and they have not, therefore, the attribute of *a separate individuality.* Various phenomena hereafter to be detailed, however, respecting the 'gemmiparous' production of living beings, when taken in connection with that just cited, seem to render it by no means impossible that the individualization may be more complete in other cases, so that independent beings of a lower type *may possibly* originate in a perverted condition of the formative operations in the higher. But no satisfactory evidence has ever been afforded by experience, that such 'equivocal generation' has actually taken-place;* and its possibility is here alluded-to, only as a contingency which it is right to keep in view. That *no higher* type has ever originated through an advance in developmental power, may be safely asserted; for, although various instances have been brought forward to justify the assertion that such is possible, yet these instances entirely fail to establish the analogy that is sought to be drawn from them.†

472. The *developmental power* which each germ possesses, under the

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* A large number of cases of this kind are enumerated by M. le Dr. Gros, in his 'Note sur la Génération Spontanée et l'Embryogénie Ascendante,' in "Ann. des Sci. Nat.," 3e Sér., Zool., Tom. XVII., p. 193; but no satisfactory evidence is given by him in regard to any one of these.

† Thus the Author of the "Vestiges of the Natural History of Creation" refers to the various modifications which have taken place in our cultivated Plants and domesticated Animals, in proof that such elevation is possible; quite overlooking the fact that these external influences merely *modify* the development, without *elevating* it, and that these races, if left to themselves, speedily revert to their common specific type. And he adduces the phenomena of metamorphosis—the transformation of the worm-like larva into an Insect, and of a fish-like tadpole into a Frog,—as giving some analogical sanction to the same doctrine; totally overlooking the fact, that these transformations are only part of the ordinary developmental process, by which the complete form of the species is evolved, instead of being transitions from the perfected type of one class to the perfected type of one above it. So, again, he quotes the transformation of the worker-grub of the Hive-Bee, into the fertile Queen, as an example of a similar advance; without regarding the circumstance that the worker is *psychically* higher (according to human ideas, at least,) than the queen, whose instincts appear limited to the performance of her sexual functions; and that the utmost which the fact is capable of proving is, that the same germ may be developed into two different forms, according to the circumstances of its early growth. It must always be borne in mind, that the character of a species, to be complete, should include *all* its forms, perfect and imperfect, modified and unmodified; since in this mode alone can that 'capacity for variation' be determined, which is so remarkable a feature in many cases, and which specially distinguishes the races of plants and animals that have been subjected to human influence. In no instance has this variation tended to confuse the limits of well-ascertained species; it has merely increased our acquaintance with the number of diversified forms into which similar germs may develope themselves.

conditions just now detailed, is primarily manifested in the *evolution* of the germ into its complete specific type, in the *maintenance* of its perfect form, and, within certain limits, by the *reproduction* of parts that have been destroyed by injury or disease. Whatever may be the variety of forms which any organism presents at different phases of its existence, these always occur in a regular series, each term of which may be considered as preparatory to the next. In most instances, the earlier forms are so obviously incomplete, that their embryonic nature is very plain; and the specific type may be considered to be represented by the fully-developed organism, in which the process of evolution culminates. But we shall meet with certain cases, in which the earlier forms have so many of the attributes of fully-developed organisms, that their incompleteness would scarcely be suspected, save from the want of the true Generative apparatus, which is usually the last set of organs to be evolved; and it is impossible, in some of these, to single-out any particular phase as that which shall be accounted the specific type, the last or culminating phase being often marked by the deficiency of organs of great importance, which were present in the earlier forms. There is always a period, however, at which the developmental power may be said to be expended; and to this succeeds, in the first instance, a stage wherein the condition last attained is preserved for a while, after which degeneration and decay supervene.—The reproduction of parts that have been lost or destroyed, as Mr. Paget has pointed-out,* differs from the ordinary process of nutrition in this, that 'in grave injuries and diseases, the parts that might serve as models for the new materials to be assimilated-to, or as tissue-germs to develope new structures, are lost or spoiled; yet the effects of such injury and disease are recovered-from, and the right specific form and composition are retained;' and, again, 'that the reproduced parts are formed, not according to any present model, but according to the appropriate specific form, and often with a more strikingly-evident design towards that form, as an end or purpose, than we can discern in the natural construction of the body.' In the reproduction of the leg of a full-grown Salamander after amputation, which was observed to take place by Spallanzani, it is clear that whilst the process was from the first of a nature essentially similar to that by which its original development took place, it tended to produce, not the leg of a larva, but that of an adult animal. Hence, it is obvious that, through the whole of life, the formative processes are so directed, as to maintain the perfection of the organism, by keeping it up, so far as possible, to the model or archetype that is proper to the epoch of its life which it has attained.

473. The amount of this Regenerating power, however, varies greatly in different classes of organized beings, and at different stages of the existence of the same being; and, as Mr. Paget has remarked (loc. cit.), it seems to bear an inverse ratio to the degree of development which has previously taken place in each case. Thus it is greatest in the Vegetable kingdom, and in the Zoophytic tribes of Animals which most closely correspond with it in the general homogeneousness of their structure and in the vegetative repetition of their organs. The *Hydra* and *Actinia* have been especially made the subjects of experiment; and by the subdivision

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* "Lectures on Surgical Pathology," Vol. I., p. 151.

(by Trembley) of one individual of the former, no fewer than fifty were produced. In this, as probably in all the cases in which new individuals have been obtained by artificial subdivision, there is some natural tendency to their production by the vegetative process of gemmation (§ 534); such, however, does not always manifest itself. It is a curious fact, that the first attempt at regeneration, in some of these cases, is not always complete; but that successive efforts are made, each of which approximates more and more closely to the perfect type. This was well seen in one of Sir J. G. Dalyell's experiments; for he observed that, having broken the stem of a *Tubularia* (a Hydroid Zoophyte), after the natural fall of its head, an imperfect head was at first produced, which soon fell-off, and was succeeded by another more fully formed; this in its turn was succeeded by another; and so on, until the fifth head was produced, which was as complete as the original.* Of the reparative power of the *Acalephæ*, nothing whatever is known; but their Zoophytic relations, and the tendency which many of them exhibit to multiply by gemmation, make it almost certain that they must possess a large measure of this regenerative capacity. Notwithstanding the rank which the *Echinodermata* possess, as the highest among Radiated animals, yet in point of development they still rank low; their bodies being made-up in a great degree of a repetition of similar parts (§ 19). Thus among Starfishes we find that one, two, or more of the 'rays' may be removed without the destruction of life, and that they are gradually regenerated; this not taking place, however, unless the central disk be preserved. Certain of the Holothuriada occasionally eject the entire visceral mass under the influence of alarm; yet they continue to move-about as if nothing had happened; and, under favourable circumstances (as appears from the observations of Sir J. G. Dalyell), they regenerate the whole of the digestive and generative apparatus thus parted-with.†

474. Next to Zoophytes, there are no animals in which the regenerative power is known to be so strong, as it is in the lower Articulata, such as the Cestoid and Trematoid *Entozoa*, the inferior *Annelida*, and the *Turbellaria* (of which the Planariæ are examples) which closely approximate to the latter of these groups; and here, again, we see that a low grade of general development is favourable to its exercise, and that the spontaneous multiplication which occasionally takes place in these animals by fission or gemmation, is only another form of the same process. In the higher forms of both these sub-kingdoms, as we no longer meet with multiplication by gemmation, so do we find that the reparative power is much more limited; the only manifestation of it among the fully-formed *Arachnida* and *Crustacea* being the reproduction of limbs, and the power of effecting even this being usually deficient in perfect Insects. The enquiries of Mr. Newport, however, upon the reproductive powers of *Myriapods* and *Insects*, in different stages of their development,‡ confirm the general principle already stated; for he has ascertained that in their *larval* condition, Insects can usually reproduce limbs or antennæ; and that Myriapods,

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* "Rare and Remarkable Animals of Scotland," Vol. I., p. 28.

† See Prof. E. Forbes's "British Starfishes," p. 199; and Sir J. G. Dalyell's "Powers of the Creator displayed in the Creation," Vol. I., chap. i.

‡ "Philosophical Transactions," 1844.

whose highest development scarcely carries them beyond the larvæ of perfect insects, can regenerate limbs or antennæ, up to the time of their last moult, when, their normal development being completed, the regenerative power seems entirely expended. The *Phasmidæ* and some other Insects of the order *Orthoptera* retain a similar degree of this power in their perfect state; but these are remarkable for the similarity of their larval and imago states, the latter being attained, as in Arachnida, by a direct course of development, without anything that can be called a 'metamorphosis.'—Little is known of the regenerative power in the higher Mollusca; but it has been affirmed that the head of the Snail may be reproduced after being cut-off, provided the cephalic ganglion be not injured, and an adequate amount of heat be supplied.—In Vertebrata, again, it is observable that the greatest reparative power is found among *Batrachian Reptiles*, whose development is altogether lower, and whose life is altogether more vegetative, than that of probably any other group in this sub-kingdom. In Fishes it has been found that portions of the fins, which have been lost by disease or accident, are the only parts that are reproduced. But in the Salamander, entire new legs, with perfect bones, nerves, muscles, &c., are reproduced after loss or severe injury of the original members; and in the Triton a perfect eye has been formed, in place of one which had been removed. In the true *Lizards*, an imperfect reproduction of the tail takes place, when a part of it has been broken off; but the newly-developed portion contains no perfect vertebræ, its centre being occupied by a cartilaginous column, like that of the lowest Fishes.

475. In the warm-blooded Vertebrata generally, as in Man, the power of true reproduction after loss or injury seems limited, as Mr. Paget has pointed-out (Op. cit., p. 164), to three classes of parts:—namely, (1). "Those which are formed entirely by nutritive repetition, like the blood and epithelia, their germs being continually generated *de novo* in the ordinary condition of the body; (2). Those which are of lowest organisation, and (which seems of more importance) of lowest chemical character, as the gelatinous tissues, the areolar and tendinous, and the bones; (3). Those which are inserted in other tissues, not as essential to their structure, but as accessories, as connecting or incorporating them with the other structures of vegetative or animal life, such as nerve-fibres and blood-vessels. With these exceptions, injuries or losses are capable of no more than repair, in its more limited sense; *i. e.*, in the place of what is lost, some lowly-organised tissue is formed, which fills-up the breach, and suffices for the maintenance of a less perfect life."—Yet, restricted as this power is, its operations are frequently most remarkable; and are in no instance, perhaps, more strikingly displayed, than in the re-formation of a whole bone when the original one has been destroyed by disease. The new bony matter is thrown out, sometimes within, and sometimes around, the dead shaft; and when the latter has been removed, the new structure gradually assumes the regular form, and all the attachments of muscles, ligaments, &c., become as complete as before. A much greater variety and complexity of actions are involved in this process, than in the reproduction of entire organs in the simpler animals; though its effects do not appear so striking. It would seem that in some individuals this re-

generating power is retained to a greater degree than it is by the class at large;* and here again we find, that in the early period of development the power is more strongly-exerted than in the adult condition. The most remarkable proof of its persistence, even in Man, has been collected by Prof. Simpson; who has brought-together numerous cases, in which, after "spontaneous amputation of the limbs of a fœtus-in-utero," occurring at an early period of gestation, there has obviously been an imperfect effort at the re-formation of the amputated part from the stump.† By the knowledge of these facts and principles, we seem justified in the conclusion, that the occurrence of supernumerary or multiple parts, even when it extends to complete duplicity of the body, is not due (as usually supposed) to the 'fusion' of two germs, but that it results from the subdivision of one. And that such is really the case, may be inferred from observations recently made upon the early phases of development of 'double monsters;' from which it appears that their production is due to the spontaneous divarication of the embryonic mass into two halves, at a grade of development which may be considered as corresponding (in regard to the homogeneity of its organisation) with the Hydra or Planaria.‡

476. There are many tribes, both of Plants and Animals, in which multiplication is effected not only *artificially* but *spontaneously*, by the separation of parts, which, though developed from the same germ in perfect continuity with each other, are capable of maintaining an independent existence, and which, when thus separated, commonly take rank as distinct individuals. This process, which is obviously to be regarded, no less than the preceding, as a peculiar manifestation of the ordinary operations of Nutrition, may take place in either of four different modes:—1. In the lowest Cellular Plants, and the simplest Protozoa, every component cell of the aggregate mass that springs from a single germ, is capable of existing independently of the rest; and thus every act of growth which consists in the multiplication of cells (§ 349), makes a

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* One of the most curious and well-authenticated instances of this kind is related by Mr. White in his work on the "Regeneration of Animal and Vegetable Substances," 1785, p. 16. "Some years ago, I delivered a lady of rank of a fine boy, who had two thumbs upon one hand, or rather, a thumb double from the first joint, the outer one less than the other, each part having a perfect nail. When he was about three years old, I was desired to take off the lesser one, which I did; but to my great astonishment it grew again, and along with it, the nail. The family afterwards went to reside in London, where his father showed it to that excellent operator, William Bromfield, Esq., surgeon to the Queen's household; who said, he supposed Mr. White, being afraid of damaging the joint, had not taken it wholly out, but he would dissect it out entirely, and then it would not return. He accordingly executed the plan he had described, with great dexterity, and turned the ball fairly out of the socket; notwithstanding this, it grew again, and a fresh nail was formed, and the thumb remained in this state."—The Author has been himself assured by a most intelligent Surgeon, that he was cognizant of a case in which the whole of one ramus of the lower jaw had been lost by disease in a young girl, yet the jaw had been completely regenerated, and teeth were developed and occupied their normal situations in it.

† These cases were brought by Prof. Simpson, before the Physiological Section of the British Association, at its Meeting in Edinburgh, Aug., 1850. The Author, having had the opportunity of examining Prof. Simpson's preparations, as well as two living examples, is perfectly satisfied as to the fact.

‡ See on this subject, Prof. Vrolik in "Brit. and For. Med. Rev.," Vol. XII., p. 374, and in "Cycl. of Anat. and Phys.," Vol. IV., pp. 973–5; Prof. Allen Thomson, "Edinb. Monthly Journal," June and July, 1844; Prof. Valentin in "Comptes Rendus de la Societé de Biologie," 1852, p. 99; and M. Lebert in "Memoires lus à la Societé de Biologie," 1852, p. 203.

corresponding augmentation in the number of (so-called) individuals.—2. In many organisms of a somewhat higher type, in which the fabric of each complete being is made up of several component parts, we find the new growths to be complete repetitions of that from which they are put forth; and thus the composite organism presents the semblance of a collection of individuals united together, so that nothing is needed but the severance of the connection, to resolve it into a number of separate and independent beings, each perfect in itself. The most characteristic example of this is presented by the *Hydra* (§ 534), which is continually multiplying itself after this fashion; for the buds or 'gemmæ' which it throws-off, are not merely structurally but functionally complete (being capable of seizing and digesting their own prey), previously to their detachment from the original stock.—3. In by far the larger proportion of cases, on the other hand, the 'gemma' does not possess the complete structure of the parent, at the time of its detachment, but is endowed with the capacity for developing whatever may be deficient. Thus, the 'zoospore' of an Ulva or a Conferva (§ 351) is nothing else than a young cell, from which the entire organism is to be evolved after it has been set free; and even in the 'bulbels' of the Marchantia (§ 492), the advance is very little greater. The 'bulbels' of certain Phanerogamic plants, on the other hand, bear more resemblance to ordinary leaf-buds (§ 508); and as these, whilst possessing the rudiments of leaves, have no roots, their capacity for independent existence depends on their power of evolving those organs.—4. In the preceding cases, the organism which is developed by this process, resembles that from which it has been put-forth; but there are many cases in which the offset differs in a marked degree from the *stock*, and evolves itself into such a different form, that the two would not be supposed to have any mutual relation, if their affinity were not proved by a knowledge of their history. Sometimes we find that the new being thus developed, is in every respect as complete as that from which it proceeded, though presenting a different type of structure; but in other instances it is made-up of little else than a generative apparatus, provided with locomotive instruments to carry it to a distance, its nutritive apparatus being very imperfect. Of the first plan, we have an example in the development of Medusæ from the Hydroid Polypes (§§ 538—544); and of the second, in the peculiar subdivision of certain Annelida, hereafter to be described (§ 576).—Now it is obvious that in this process, no agency is brought into play, that differs in any essential in mode from that which is concerned in the ordinary nutritive operation. The multiplication of independent beings is performed exactly after the same fashion as the extension of the original stock; and the very same parts may be regarded as organs belonging to *it*, or (in ordinary phraseology) as new individuals, according to their stage of development, and the relation of dependence which they still hold to it. The essence of this operation is *the multiplication of cells by continual subdivision* (§ 349).

477. We have now, on the other hand, to enquire into the nature of the true *Generative* process, by which the original germ is endowed with its developmental capacity; and this we shall find to be of a character precisely the opposite of the preceding. For, under whatever circumstances the generative process is performed, it appears essentially to

consist in *the reunion of the contents of two cells*,* of which the germ, which is the real commencement of a 'new generation,' is the result. This process is performed under the three following conditions—1. Any of the cells of the entire aggregate produced by the previous subdivision, may be capable of thus uniting with each other indiscriminately; there being no indication of any sexual distinction. This is what we see in the simplest Cellular plants (§ 481).—2. Any of the component cells of each organism may, in like manner, pair with other cells, to produce fertile germs; but there are differences in the shares which they respectively take in the process, which indicate that their endowments are not precisely similar, and that a sexual distinction exists between them, notwithstanding that this is not indicated by any obvious structural character. This condition is seen in the *Zygnema* and its allies (§ 483).—3. The generative power is restricted to certain cells, which are set-apart from the rest of the fabric, and destined to this purpose alone; and the endowments of the two sets are so far different, that the one furnishes the germ, whilst the other supplies the fertilizing influence; whence the one set have been appropriately designated 'germ-cells,' and the other 'sperm-cells.' Such is the case in all but those lowest Plants which have not a specialized generative apparatus; and also throughout the Animal kingdom.

478. Thus, then, in the entire process in which a new being originates, possessing like structure and endowments with its parent, two distinct classes of actions participate,—namely, the act of *Generation*, by which the germ is produced,—and the act of *Development*, by which that germ is evolved into the complete organism. The former is an operation altogether *sui generis;* the latter is only a peculiar modification of the Nutritive function; yet it may give origin, as we have seen, to numerous independent offsets, by the separation (natural or artificial) of the parts which are capable of existing as such. Now between these two operations there would seem to be a kind of antagonism. Whilst every act of Development tends to *diminish* the 'germinal capacity,' the act of Generation *renews* it; and thus the tree which has continued to extend itself by budding until its vital energy is well-nigh spent, may develope flowers, and mature seeds, from which a vigorous progeny shall spring-up. But *multiplication* does not directly depend upon the act of generation alone; it may be accomplished by the detachment of *gemmæ*, whose production is a simple act of development; and the independent beings thus produced are sometimes similar, sometimes dissimilar, to those from which they sprang. When they are dissimilar, however, the original type is always reproduced by an intervening act of generation; and *the immediate products of the true generative act always resemble one another.* Hence the phrase 'alternation of generations' can only be legitimately employed, when the term generation is used to designate a succession of (so-called) individuals, by whatever process they have originated; an application of it which cannot but lead to a complete obliteration of the essential distinction which the attempt has been here made to draw, between the Generative act and the Developmental act of gemmation. For when it

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* In very rare instances, it is the reunion of the two parts of the contents of the same cell, which had previously tended to separate from each other, as if in the process of subdivision (§ 482).

is said that 'generation A produces generation B, which is dissimilar to itself, whilst generation B produces generation C, which is dissimilar to itself, but which returns to the form of generation A,'* it is entirely left out of consideration, that generation A produces (the so-called) generation B by a process of *gemmation;* whilst the process by which generation B produces generation C, is one of *true generation.* So generation C, by gemmation, developes D, which resembles B; and D, by a true generative act, produces E, which resembles A and C. This distinction, although it may at first sight appear merely verbal, will yet be found of fundamental importance in the appreciation of the true relations of these processes, and of their resulting products.—So, in the Author's opinion, the application of the term 'a generation' to the *entire product* of the development of any germ originating in a generative act, whether that product consist of a single individual, or of a succession, will be found much more appropriate, and more conducive to the end in view, than the indiscriminate application of it to each succession, whether produced by gemmation or by sexual reunion. It is of great importance to the due comprehension of certain phenomena of Reproduction, which will come under consideration in the Animal kingdom, that the relations of the products of these two processes should be rightly appreciated; and this appreciation of them will, it is believed, be best gained by a careful enquiry into the phenomena of Reproduction in the Vegetable kingdom.

2. *Generation and Development in Plants.*

479. Our knowledge of the reproductive process in the Vegetable Kingdom has of late been greatly extended by Microscopic research; and although it is not possible at present to give a complete sketch, much less a full account, of the mode in which it is performed in all the principal groups of Plants, still enough has been ascertained in some of the most important, to make it probable that the general doctrines founded upon the phenomena which they present, may be applied to those whose history has been less completely studied. It may be stated as a certainty, that the true Generative act is not confined, as was long supposed by most Physiologists, to the *Phanerogamia* or Flowering Plants; but that it is performed by so many of the *Cryptogamia,* that its universality can scarcely be a matter of legitimate doubt. So far as our present knowledge extends, this generative act may be performed in three distinct modes, each of which is peculiar to a certain assemblage of Plants.—The *first* of these is the 'conjugation' of two apparently *similar* cells, and the admixture

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* Such is the doctrine propounded in the highly original and ingenious work of Prof. Steenstrup on the "Alternation of Generations," a translation of which has been published by the Ray Society.—The Author feels satisfied, from careful and repeated consideration of the phenomena on which this doctrine is founded, that it cannot be accepted in its original form, and that it requires to be modified in the manner indicated in the text. His reasons for this modification, and likewise for his dissent from the hypothesis put forth by his friend Prof. Owen in his treatise on "Parthenogenesis," will be found in the "Brit. and For. Med.-Chir. Rev." vol. i. p. 183, and vol. iv. p. 436. It has been with the greatest satisfaction that he has found his views on this subject fully participated-in by his friend Mr. T. H. Huxley, who has adduced various important considerations in their support, in his Memoir 'On the Anatomy of Salpa and Pyrosoma,' "Philos. Transact.," 1851, pp. 576—579; see also the outline of his Lecture 'On Animal Individuality,' in "Ann. of Nat. Hist." 2nd Ser. Vol. IX., p. 505.

of their contents, whereby a new body, the 'primordial embryo-cell', is produced; a method which seems peculiar to the *Protophyta*. This conjugation, however, may occur in one of three distinct modes (Fig. 191, A).

Fig. 191.

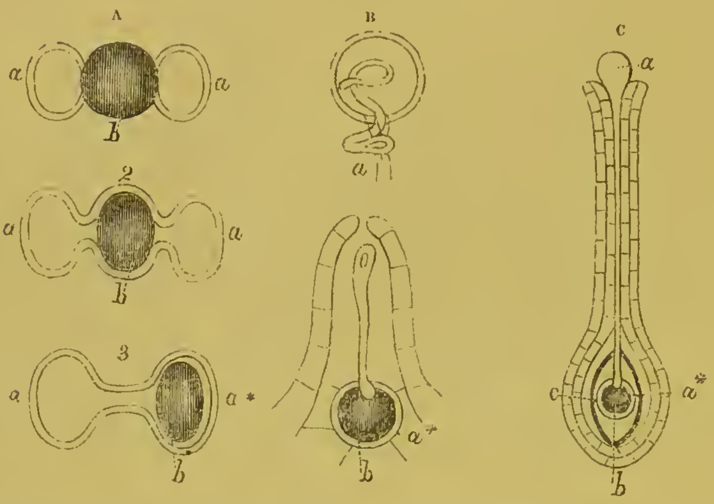


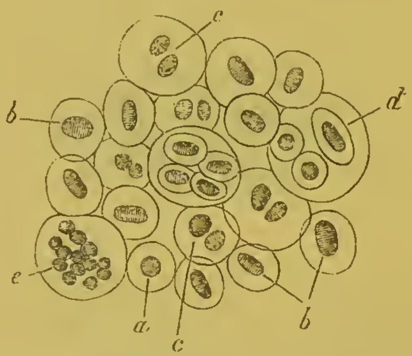
Diagram representing the three principal forms of the *Generative Process in Plants*:—A, conjugation of inferior Cryptogamia; formation of the embryo-cell, *b*, by admixture of the discharged endochromes of the parent-cells, *a*, *a*; 2, production of the embryo-cell, *b*, within a dilatation formed by the union of the two parent-cells; 3, production of the embryo-cell, *b*, by the passage of the endochrome of cell *a* into that of cell *a**, marking-out a sexual difference.—B, fertilization of germ in higher Cryptogamia; *a*, sperm-cell discharging its spiral filament, *a**, germ-cell, against which one of these filaments is impinging; *b*, embryo-cell produced by their contact.—C, fertilization of germ in Phanerogamia; *a*, sperm-cell, or pollen-grain, sending its prolonged tube down the style, until it reaches *a** the germ-cell, inclosed in the ovule, the section of whose coats is shown at *c*; from the contact of the two is produced the embryo-cell *b*.

Both the cells (1, *a*, *a*) may rupture and discharge their contents; and around the mass (*b*) formed by their intermixture, the cell-wall, by which it is constituted the 'embryo-cell,' is developed. The union of the contents of the conjugating cells may take place, on the other hand, without their external discharge, by the establishment of a direct passage between them; and the intermixture may occur, either within the connecting channel (2), or in one of the cells of the pair (3), the new cell-wall being formed, as before, around the blended mass. In this last form, the 'embryo-cell' being developed within one of the conjugating cells, the distinction between 'sperm-cells' and 'germ-cells' is apparently foreshadowed.—In the *second* case, the generative act is effected by the agency of cells which are manifestly *dissimilar* in their endowments; for the one set develope within themselves certain moving filaments, that convey their influence to the cells of the other set, within which last the 'embryo-cell' originates; so that the distinction between 'sperm-cells' and 'germ-cells' is here characteristically shown (Fig. 191, B). This is the mode in which the generative act seems to be performed in all the *Cryptogamia* save the Protophytes; the embryo-cell being at once thrown upon the world in the inferior groups, and being dependent for its supply of food upon its own absorbing and assimilating powers; whilst in the superior, it is supplied for a time with nutriment prepared and imparted to it by its parent.—In the *third* form of the generative process

(Fig. 191, c), which is peculiar to *Phanerogamia*, there is the same distinction between 'sperm-cells' and 'germ-cells,' but the mode in which the action of the former upon the latter is brought-about is different; for the 'sperm-cell' (*a*) does not evolve self-moving filaments, but puts forth long tubes, which extend themselves until they reach the 'germ-cell' (a^*), and thus convey to it the fertilizing influence. Moreover, the germ, which takes its origin from the 'embryo-cell' developed within the 'germ-cell,' is supplied with nutriment by its parent, not merely whilst it remains in connection with the organism which evolved it, but for some time subsequently; its continued growth being provided-for by the store laid-up around it in the *seed;* and it being at the expense of the materials which it thence obtains, that the germ is enabled to develope and put-forth the first of those organs, which are subsequently to act as its own instruments of absorption and assimilation.—Each of these processes will now be described in more detail.

480. It is among the lowest tribes of Plants, that we see the closest relation between the functions of Nutrition and Reproduction. For we do not here find, as in the higher Plants, that the development of distinct *organs* is requisite, to enable the descendants of the original germ-cell to exist independently of each other; since this power is possessed by every one of the cells that are produced by its fission (§ 349), so that they have the same title to be accounted independent existences, as have the leaf-buds of the Flowering-plant. Thus, a frond of the *Coccochloris cystifera*, one of the simple Algæ belonging to the family *Palmelleæ*, presents us with a mass of independent cells, held together by a common mucous investment (Fig. 192); and in such a mass we usually find cells in various stages of development. At *a* is seen a simple globular cell, surrounded by a well-defined mucous envelope: at *b* are cells which present an elongated form, and are evidently about to undergo subdivision: at *c* we observe a pair of cells, whose separation has apparently been recent, as they are still surrounded by the same mucous envelope: at *d* we have a group of three cells, each having its own mucous envelope, but all of them still held-together by the original investment; the two smaller of these cells are obviously produced by a secondary subdivision of one of the first pair; whilst the other shows by its elongated form that it is about to subdivide: and at *e* is a group of small cells formed by a continuance of the same subdividing process, each of them subsequently increasing in size, acquiring a mucous envelope of its own (as at *a*), and in its turn going through the same series of changes. And as this will take place equally, whether the cell be detached from the general mass, or remain as a component part of it, it must be accounted a distinct 'individual,' in the ordinary acceptation of that term. But as it will be shown hereafter, that the entire mass of independent cells thus generated is

FIG. 192.

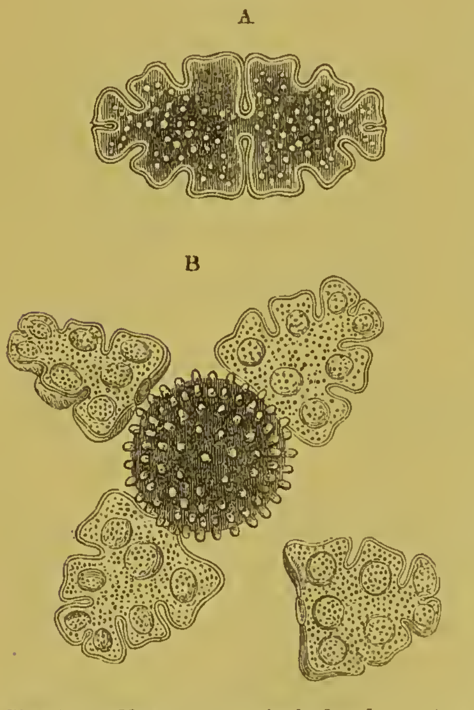


Multiplication of *Coccochloris cystifera* by subdivision of cells; *a, b, c, d, e,* various stages of development.

the homological equivalent of the single embryo of a Phanerogamic plant, the component cells of which are mutually dependent, the term 'individual' cannot be legitimately applied to both alike; and it will be found convenient, therefore, to distinguish the independent beings which are thus related as the products of a single generative act, by the appellation of 'phytoids' (see § 516.)—To what extent this method of multiplication may proceed, has not been ascertained. There is reason to think that there is a limit to its performance, since we find it giving place, at a certain period of the year, to the converse process; namely, the true Generative act. But upon the principle already laid down, we should expect that it may be carried-on to a vast extent, under favourable circumstances; since there is here no advance upon the very simplest condition of an organised structure, and consequently but little exhaustion of the 'germinal capacity' (§ 469).

481. As amongst the independent cells of which the simplest Algæ are composed, each seems capable of going through the whole series of Nutritive operations *for* and *by* itself, so there is no perceptible difference in their endowments as regards the Generative act; the process of 'conjugation' appearing to take place indifferently amongst any pair of them. As examples of this process, two instances will be first selected from the families of *Desmideæ* and *Diatomaceæ;* in which its occurrence is a fact of peculiar interest, as tending to show their close alliance to the simpler Algæ, from which they have been separated by Prof. Ehrenberg and other naturalists, who have considered them deserving of a place in the Animal kingdom.—The *Desmideæ* are characterised by the peculiar structure of their cells; for the wall of each consists of two distinct and symmetrical valves, united to each other by a transverse suture; and the endochrome shows a tendency to separation into two equal halves at the same part. In some instances there is a constriction at the suture, so that the two portions of the cell are connected only by a narrow neck, as in *Euastrum* (Fig. 193 A); but in other cases, as in *Closterium*, the median portion traversed by the suture is the broadest part of the cell. The plants of this family are generally met-with in the condition of detached cells or 'fronds;' but in some instances, these are associated into confervoid filaments; the difference simply arising from the continuance, in the latter case, of that connection between the cells that have been multiplied by subdivision, which is broken in the former by their separation. The first stage in the conjugating process is the approximation

FIG. 193.



Euastrum oblongum:—A, single frond;—B, two fronds in conjugation, showing the spore in the centre between the four emptied valves.

of two cells, in whose contained granules an active movement is often seen at the same time. Each of the two cells then gives way at the plane of its transverse division (B), and the four halves discharge their contained 'endochromes' into the central space, so that those of the two cells are thus completely incorporated. At first the new mass is merely surrounded by the mucous envelope, and has no definite shape; but it soon becomes invested by a distinct cell-wall, which presents a regular form, usually globular or spheroidal; and this cell-wall, which is generally very firm, is often furnished with curious prolongations which give it a hispid surface (as seen at B), these being sometimes very long, and furnished with hooks at their extremities. The new body thus formed is properly the 'primordial cell' of the embryo;* and it originates a new generation by the ordinary process of subdivision, the firm outer case first giving way, to allow of the expansion of its contents, around which a new and more delicate cell-wall has been previously developed. It has been remarked that the spores of the Desmideæ (which are for the most part inhabitants of small collections of fresh water, that are liable to be dried-up by the heat of summer,) are most abundant in spring; so that it may be surmised that they are not killed by desiccation, like the growing fronds, but are enabled to regenerate the race after the period of drought has passed away.—The mode in which the conjugation and development of the spores take place in the entire family of *Desmideæ*, is essentially the same; and even where the cells that have been multiplied by subdivision remain in continuity with each other, so as to form a filament, they dissociate themselves before the conjugation takes place. Sometimes it is observable, that instead of the complete separation of the two halves of each cell in the act of conjugation, they only partially open for the discharge of the endochrome; and in some of the higher forms of this family, we find the mixture to take place in one of the conjugating cells, within which the spore is developed. This happens especially in the genus *Desmidium*, which approaches closely to the conjugating Confervæ.†

482. In the family *Diatomaceæ*, the membranous envelope of each cell is covered by a siliceous incrustation, which usually presents very beautiful and regular markings; and this hard 'shell' is composed of two 'valves,' which are divided longitudinally, and are capable of being separated from each other. Like the plants of the preceding family, the cells may occur either singly (Fig. 194, A, B), or in connection with each other; in the first case they are known as 'frustules;' in the second they form bands or filaments composed of several cells adherent by their long sides, which cells have all been produced by subdivision from a single one, and have not become detached from each other. When two frustules (as in *Eunotia turgida*) are about to enter into conjugation, they move towards each other, and come into close approximation by their concave edges (C); the valves of each frustule separate from each other (D), and the inner membrane forms two protuberances, which meet two

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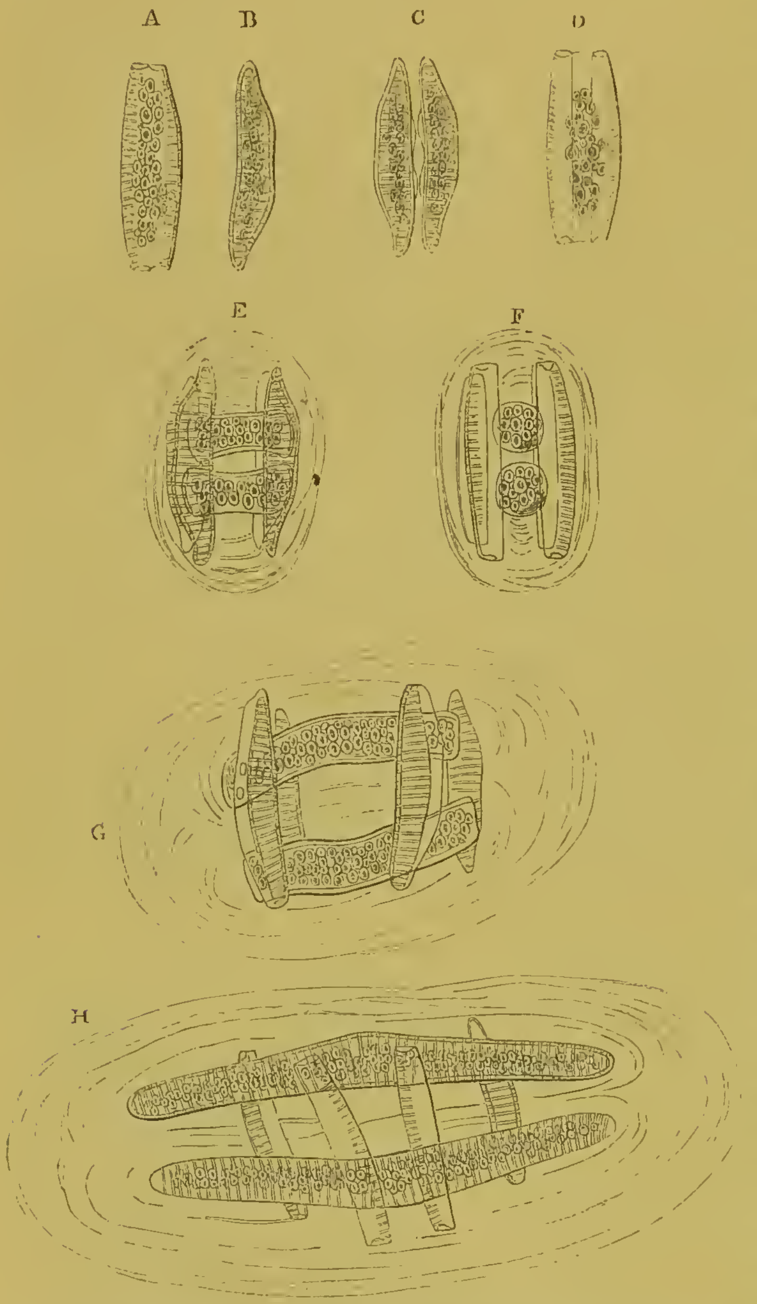
* This body is commonly termed the 'sporangium;' but the author agrees with his friend the Rev. W. Smith, in considering that where only a single cell is formed as the immediate product of the conjugating act, this has no just claim to the title. (See "Transact. of Microsc. Soc.," 2nd Ser., Vol. I., p. 68).

† See Mr. Ralfs's admirable Monograph on the "British Desmideæ."

similar ones of the other frustule. These protuberances soon give way, and the endochromes of the two frustules discharge themselves and mingle, not, however, into *one* mass, but into *two;* these masses are at first irregular in shape; but they shortly become covered with a smooth membrane, and possess a symmetrical elongated form (E, F), which presents some resemblance to that of the parent frustule. These spore-cells continue to increase in length (G), and at last they acquire the transverse markings of the parent frustules, which they greatly exceed in dimensions (H). These large embryonic frustules seem to give origin to a new brood, by the ordinary fissiparous multiplication; and it may be conjectured that this process cannot take place indefinitely, but that the race would die out, were it not for the renewal of the powers of growth by the act of conjugation.—In the *Meloseireæ,* which constitute a filamentous tribe of Diatomaceæ, there is a curious departure from the ordinary type; for no conjugation can be here seen to occur between

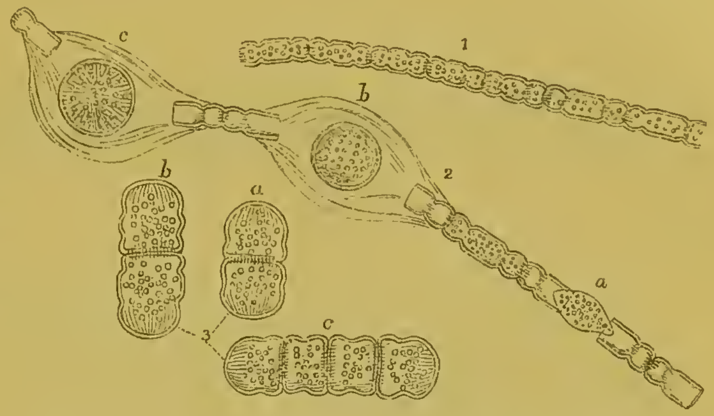
Fig. 194.



Conjugation of *Eunotia turgida:*—A, single frustule; B, side view of the same; C, two frustules with their concave surfaces in close apposition; D, front view of the same, showing the separation of each frustule longitudinally into two halves; E and F, side and front views after the formation of the embryo-cells; G, the embryonic frustules more advanced, exceeding the parent-frustules in size; H, completion of the embryonic frustules.

two distinct frustules; but a disturbance of a somewhat equivalent nature takes place in the endochrome of a single frustule, its particles moving from the extremities towards the centre, rapidly increasing in quantity, and aggregating into a mass, round which a new envelope is developed, so that it becomes a 'primordial-cell' resembling that of other plants of its kind (Fig. 195). At first sight, this might seem an exception to the general rule of the reunion of the contents of *two* cells; but it is more so in appearance than in reality. For in some of the group of *Conjugateæ*, whose conjugation will be presently described (§ 483), the union of endochromes takes place, not between the cells of distinct filaments, but between two contiguous cells of the same filament; and as these two cells formed part of one and the same cell previously to their separation by its subdivision, it is obvious that the reunion of the two halves of the endochrome in the Meloseireæ is only the performance of the same process at an earlier period. The spore thus formed is gradually developed into a filament resembling that of the parent, by progressive fissiparous multiplication (Fig. 195, 3, *a*, *b*, *c*).*

FIG. 195.



Development of spores, or primordial embryo-cells, in *Aulacoseira crenulata*:—1, simple filament, 2, filament developing spores; *a*, *b*, *c*, successive stages in the formation of spores;—3, embryonic frustules, *a*, *b*, *c*, in successive stages of multiplication.

483. The process of 'conjugation' has now been seen to occur in so many species of the family of *Palmelleæ*, which includes the uni-cellular forms of the ordinary Algæ (such as the *Hæmatococcus*, Fig. 162, the *Protococcus*, to which the 'red snow' belongs, the *Coccochloris*, Fig. 192, the *Palmella*, of which one species is known as the 'gory dew,' and many others), that it may be regarded as a part of the regular series of vital actions in every member of that group.—It is, however, in the *Zygnema* and its allies, constituting the family of *Conjugateæ*, that this phenomenon has been longest known and most attentively studied. All these plants are filamentous; that is, the process of subdivision always takes place in the same direction, and the cells thus produced remain in continuity with each other; so that, from a single cell, a long filament is evolved (Fig. 196, A). Still the component cells of this filament for the most part retain their common relation to the generative as well as to the nutritive function, so that they may all take a share in the conjugating process: the only exception to this yet noticed, being in the case of two species of *Zygnema*, in which the alternate cells alone conjugate.† The conjuga-

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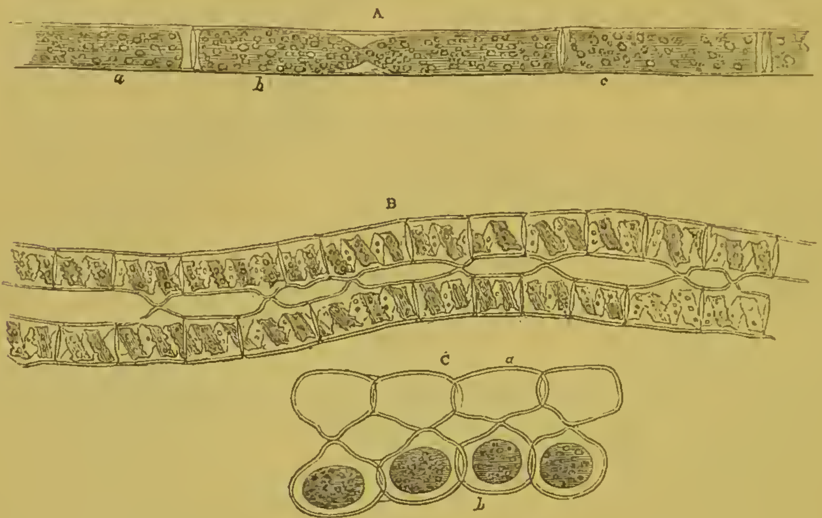
* See Mr. Thwaites's valuable Memoirs 'On the Conjugation of the Diatomaceæ,' in "Ann. of Nat. Hist.," Vol. XX., and 2nd Ser., Vol. I.

† See Dr. Hassall's "British Fresh-water Algæ," p. 139.

tion ordinarily takes place between the cells of distinct filaments; these approximate each other, and put-forth little protuberances that coalesce and establish a free passage between the cavities of the cells, whose contents then intermingle (B). In the true *Zygnema*, the endochrome of one

Fig. 196.



Various stages in the Generation of *Zygnema quininum*:—A, three cells *a*, *b*, *c*, of a young filament, of which *b* is undergoing subdivision; B, two filaments in the first stage of conjugation, showing the spiral disposition of their endochromes, and the protuberances from the conjugating cells; C, completion of the act of conjugation, the endochromes of the cells of the filament *a* having entirely passed over to those of filament *b*, in which the spores are formed.

cell passes-over entirely into the cavity of the other; and it is within the latter that the embryo-cells are formed (C). Further, it may generally be observed that *all* the cells of one filament thus empty themselves, whilst *all* the cells of the other filament become the recipients: here, therefore, we seem to have a foreshadowing of the *sexual* distinction of the generative cells, which manifests itself more fully in the higher organisms.* In the genus *Mesocarpus*, however, and some other Conjugateæ, the two cells pour their endochromes into a dilatation of the passage that has been formed between them; and it is there that the spore is formed.—There are several tribes of the family Conjugateæ, in which the conjugation takes place between the adjacent cells of the same filament; each cell of the conjugating pair putting-forth a conical protuberance near the septum, and the two protuberances uniting, so as to permit the mixture of endochromes, as in other instances, the spore being formed within one of the cells. Hence, when one of these filaments is 'in fruit,' the alternate cells will be found to contain spores, whilst the intermediate ones will be entirely empty.—In all these cases, the development of the new filament appears to take place by the subdivision of the 'primordial cell,' as in the instances already described; and this subdivision occurs in some instances in the immediate product of the conjugation, so that a number of smaller cells are formed, in the stead of a single large one.*

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* It is affirmed by Itzigsohn, that within certain of the filaments of *Spirogyra*, the endochrome breaks up into little spherical aggregations, which are gradually converted into nearly-colourless spiral filaments having an active spontaneous motion, and therefore analogous to the 'antherozoids' of the higher Algæ. (See "Ann. des Sci. Nat.," 3e Sér., Botan., Tom. XVII., p. 150.) More precise observations, however, are needed, to determine the relation of this phenomenon to the generative process.

484. In a considerable proportion of the inferior *Algæ*, a multiplication of 'phytoids' is effected by a very different process; namely, the separation and dispersion of 'zoospores.' These bodies are formed without any conjugation, and they originate, in fact, in the *subdivision* of the cells from which they are set-free (§ 351). The whole history of these bodies shows, that they are not products of a true generative act, but are merely to be regarded as detached *gemmæ*, formed by a developmental process. For whilst, in the ordinary process of subdivision, the endochrome of each cell divides into only two parts, and these, when completely separated by a new cell-wall, remain in contiguity within their common envelope, the 'zoospores' are formed by a subdivision of the endochrome into a greater number of parts, each of which acquires a cell-wall of its own; and all the young cells thus produced escape from the general investment, and undergo dispersion by the exercise of the locomotive power with which they are endowed.—Such is the only method of reproduction which has yet been observed in the *Ulvæ* and a considerable number of *Confervæ*. But there is a strong probability from analogy, that a conjugating process takes place even amongst these at *some* stage of their existence; for it does not seem possible that the multiplication by gemmation can go-on to an *unlimited* extent in these lower organisms, any more than in the higher. It may perhaps be surmised without any great improbability, that the process of conjugation does not take place among the cells of the *complete* plant, but in some earlier stage of development. In fact, the early stage of the *Confervæ* and *Ulvæ* so strongly resembles the permanent condition of the *Palmelleæ* (Fig. 192), that it is not impossible that some of what have been supposed to be conjugating cells of the latter group, may really belong to the former. For the complete history of the development of the embryo-cells is as yet so far from having been made out, that it is by no means certain that those which result from the conjugation of a supposed Palmella or Coccochloris, may not develope themselves into an Ulva or Conferva; and when the phenomena of reproduction in the higher Algæ (§ 485) are compared with those which present themselves in the Ferns (§ 494), it will be seen that there is a strong analogical probability in favour of such a view.—This point is one peculiarly deserving of further investigation.

485. In passing to the higher *Algæ*, we encounter a very marked change in the mode in which the Generative act is performed; the essen-

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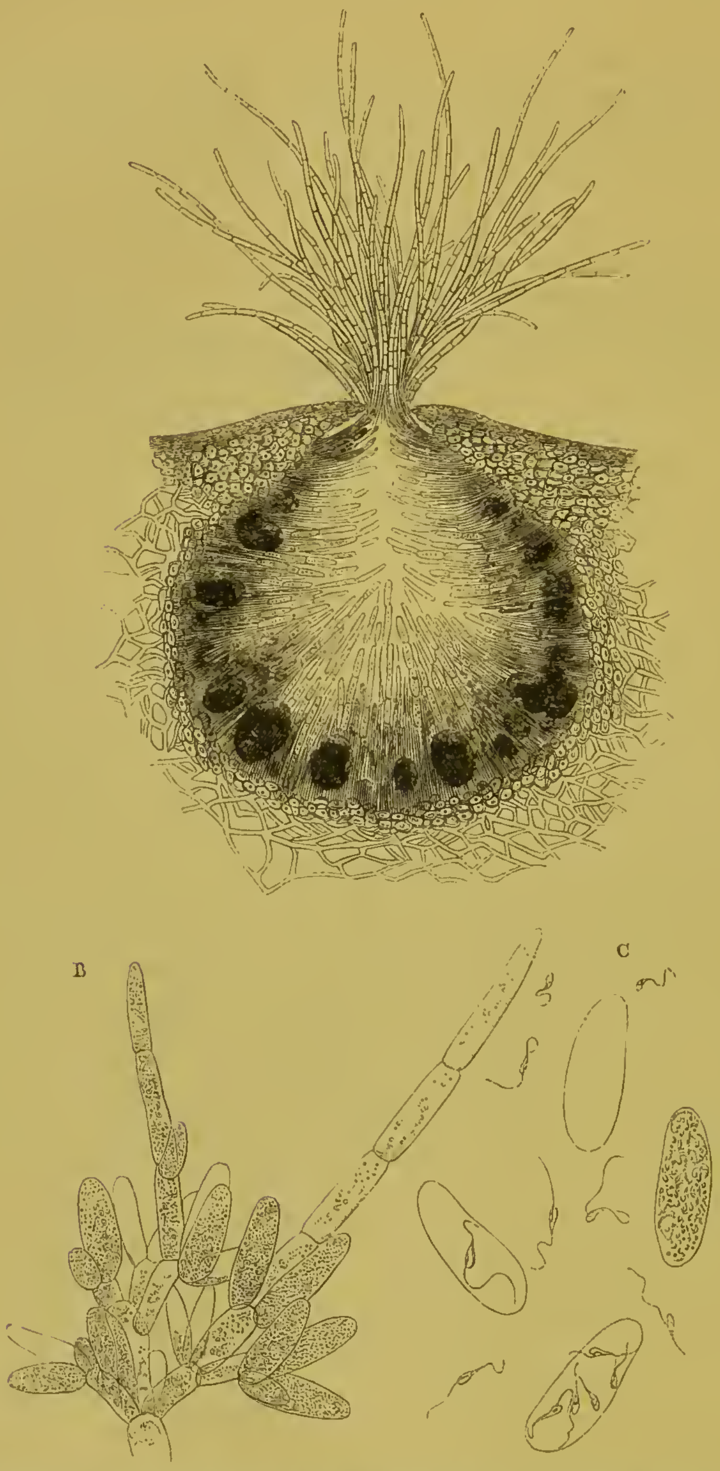
* See Dr. Pringsheim 'On the Germination of the Spores of *Spirogyra*,' in "Ann. of Nat. Hist.," 2nd Ser., Vol. XI., pp. 210, 292; also the Rev. W. Smith 'On the Germination of the Spore in the *Conjugateæ*,' Op. cit., Vol. VIII., p. 480, and 'On the Stellate Bodies occurring in the Cells of Fresh-water Algæ,' in "Microsc. Transact.," 2nd Ser., Vol. I., p. 68.—It is a very curious feature in the history of these humble Plants, that there should be such an absence of constancy in the mode in which this function is performed. It is remarked by Dr. Pringsheim that various forms of spore may be formed in the same plant, and out of the same contents destined for reproduction, although there is for each species one normal form, that is distinguished by the preponderating frequency of its occurrence. So it is observed by Mr. Smith, of the very act of conjugation, that "although one mode of effecting the union of the cells seems to be pretty general in the same Alga, it is by no means constant, as tubes connecting contiguous cells of the same filament, or uniting apposed cells of other filaments, will be found in connection with the same species."

tial character of it, however, still remaining the same. In the structure of these plants, as formerly pointed-out (§ 249), we no longer meet with

Fig. 197.



A, vertical section of a conceptacle of *Fucus platycarpus*:—B, branching articulated hairs, detached from the wall of the conceptacle, bearing antheridia in different stages of development:—C, antherozoids, some of them free, others still included in their antheridia.

the same homogeneousness as in the simpler tribes; the frond has a definite form and structure in each species, instead of being a mere amorphous mass; the several cells composing it no longer repeat each other, but exhibit a great variety of forms and modes of aggregation; and they no longer possess a capacity for independent existence. The Generative function is now limited to particular portions of the fabric; and the sexual distinction between the 'sperm-cells' and the 'germ-cells' becomes apparent. The 'germ-cells,' within which the 'embryo-cells' that give origin to the new generation are to be formed, are commonly found in the interior of 'conceptacles' (Fig. 197, A) lined with filamentous cells, the contents of which appear to be gradually absorbed into the germ-cells, so that whilst the latter increase, the former are emptied and shrink, sometimes at last disappearing altogether. The 'sperm-cells' (B) are distinguished, towards the period of their maturity, by the peculiar appearance of their granular contents, which present an orange-hue, and gradually shape themselves into oval bodies, each with an orange-coloured spot, and with two long filiform appendages (C), which, when discharged by the rupture of the containing cell, have for a time a rapid undulating motion, whereby these spermatoid particles or 'antherozoids' are dispersed through the surrounding water. The 'sperm-cells' are sometimes contained within the same conceptacles as the 'germ-cells' (as in *Fucus canaliculatus*), though they may occupy different parts of their cavity (as in *F. tuberculatus*); when developed within distinct conceptacles, these two sets of organs, which may then be designated 'antheridia' and 'pistillidia,' are sometimes developed upon the same individuals (as occasionally in *F. nodosus*), in other cases upon different plants (as in the common *F. vesiculosus**). These variations foreshadow the diversities in the disposition of the sexual organs in the Phanerogamia; and it is highly interesting to see the monœcious, the diœcious, and the hermaphrodite arrangements thus presenting themselves in the very lowest plants in which a distinction of sexes is clearly manifested.—Although the precise manner in which the influence of the 'antherozoids' is exerted upon the contents of the 'germ-cells' has not yet been made-out, the fact seems to have been demonstrated, that such influence is necessary for the production of fertile spores. For it has been found by M. Thuret, that if the 'sperm-cells' and 'germ-cells' of the diœcious species of Fuci be collected and kept separate, no development occurs from the latter, although they may put forth irregular prolongations as if about to germinate. But when they are mingled together, the 'antherozoids' attach themselves to the 'germ-cells,' crawl as it were on their surface, and communicate to them a rotatory movement by the vibration of their own filaments. In the course of a day or two, the 'primordial cell' or 'spore' formed within the germ-cell becomes invested with a distinct membrane or 'perispore,' and soon begins to undergo duplicative subdivision; by the continuance of which process, a cellular mass with a kind of radical filament is formed, from which the young plant is progressively evolved.* In some instances, however, the first cells formed by this process separate from one another, being set-free by the rupture of the perispore; and each of them may give origin to an independent plant or 'phytoid.' In this manner, 2, 4, or 8 'phytoids' may be produced, according as the separation takes place after the first, the second, or the third subdivision.†—It is only in the higher Algæ, however, that 'sperm-cells' and 'germ-cells' are thus included within distinct conceptacles, developed from particular portions of the frond; for these, in the lower tribes, are neither distinctly separated from the surrounding tissues, nor are they limited to any special parts of the surface of the frond.

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* It was at first stated by MM. Thuret and Decaisne, that *Fucus vesiculosus* sometimes has its 'sperm-cells' and 'germ-cells' associated in the same conceptacles, sometimes limited to different individuals; but they now affirm that the latter condition only is presented by the true F. vesiculosus, the former being characteristic of another species, *F. platycarpus*, previously confounded with it.

486. Besides the true generative process which has been now described, the Algæ are generally (probably universally) furnished with a means of *multiplication*, by the production of *gemmæ*, which detach themselves from the stock, and are developed into separate 'phytoids.' In a large proportion of the group, these gemmæ correspond with the 'zoospores' of the Protophyta (§ 484); being provided with numerous vibratile filaments, or cilia, by the movements of which they are dispersed through the water.‡ There is such a resemblance, in some instances, between these 'zoospores' and the 'antherozoids' just described, that they might be readily confounded together; their physiological difference, however, is most complete, since every 'zoospore' may develope itself into a new 'phytoid,' whilst the 'antherozoids' can themselves produce nothing, their influence being only exerted in fertilizing the 'germ-cells.'—But in the large order *Florideæ,* the plants composing which are for the most part of a red or reddish colour, the gemmæ have no self-moving power; and in consequence of their usually occurring in groups of four (Fig. 198, B), they are known as 'tetraspores.'§ These are generally immersed in the

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* "Comptes Rendus," Avril 25, 1853, and "Ann. of Nat. Hist." 2nd Ser., Vol. XII., p. 64.

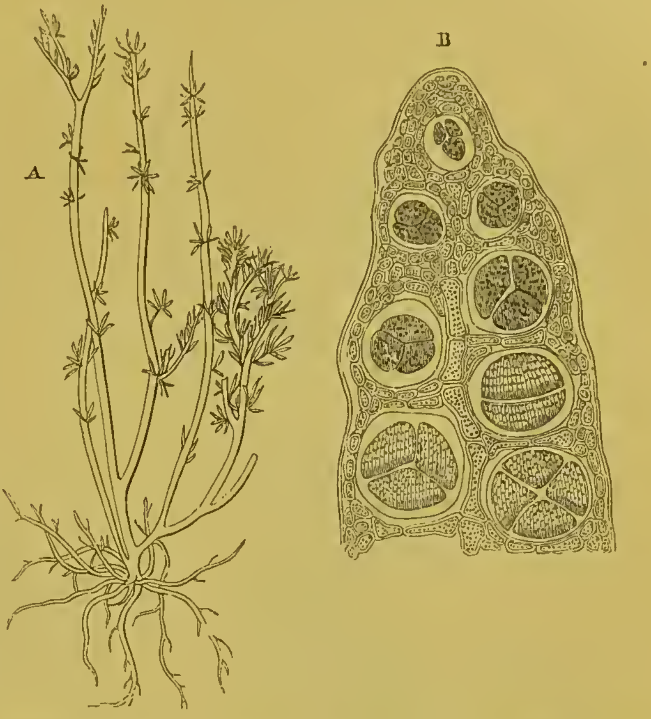
† The first great advance towards our present knowledge of the sexual reproduction of the higher Algæ, was the discovery of the *antheridial* character of certain of the conceptacles of the Fucaceæ, made by MM. Decaisne and Thuret in 1844 ("Ann. des Sci. Nat.," 3e Sér., Botan., Tom. III.); and on this discovery Dr. Harvey proceeded, so far as he was justified in doing, in remodelling the arrangement of the class ("Manual of the British Marine Algæ," 1849). A most valuable series of observations has been subsequently made by M. Thuret and MM. Derbès and Soulier ("Ann. des Sci. Nat.," 3e Sér., Botan., Tom. XIV., XVI.); and the experiments of the former of these excellent observers have now furnished the *proof* of sexuality which was previously deficient.

‡ The discovery that a large proportion of the highest Algæ (including the *Fucaceæ* and their allies) multiply, like the Protophyta by 'zoospores,' has been recently made by M. Thuret. See his 'Recherches sur les Zoospores des Algues,' in "Ann. des Sci. Nat.," 3e Sér., Botan., Tom. XIV.

§ Much discrepancy of opinion has existed in regard to the homology of the 'tetraspores' of the *Florideæ;* the history of their evolution not having been accurately followed-out. By Agardh, Decaisne, and some other distinguished Algologists, they have been regarded as the generative spores; whilst the conceptacular spores have been regarded as gemmæ. The view taken above, which is that first propounded by Mr. Thwaites, and adopted by Dr. Harvey ("Manual of British Marine Algæ," 2nd Edit., p. 68), is supported by the fact since established by M. Thuret ("Ann. des Sci. Nat.," 3e Sér., Botan., Tom. XVI., p. 14), that the antheridia and the generative (conceptacular) spores occupy corresponding parts of different plants. It is remarkable that, according to the observations of M. Thuret, the 'antherozoids' of the *Florideæ* should agree with their 'tetraspores,' in being destitute of the cilia possessed alike by the 'antherozoids' and by the 'zoospores' of the *Fucaceæ.*

substance of the frond, sometimes congregating, however, in particular parts, or being restricted to a special branch (Fig. 14); they are seldom included in distinct conceptacles, and are in this respect unlike the true generative spores. Each group seems to be evolved within one of the ordinary cells of the frond, which undergoes a duplicative subdivision; the four secondary cells thus formed, however, remain enclosed within their primary cell until the period of maturity, a new envelope of a semi-gelatinous character, the 'perispore,' being formed around them. The dispersion of these tetraspores can only be effected by the movements of the water into which they are emitted by the rupture of the perispore.

Fig. 198.

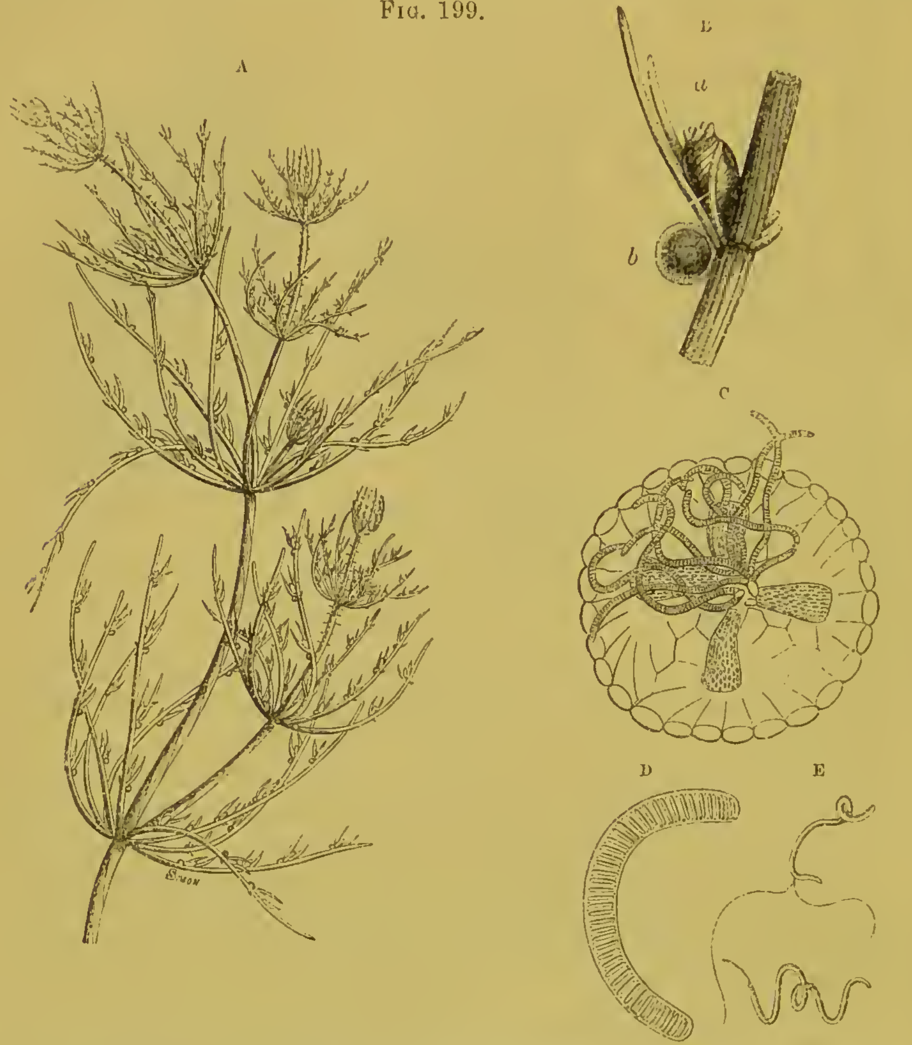


Structure of *Carpocaulon mediterraneum*:—A, entire plant; B, longitudinal section of branch, with tetraspores.

487. The Generative apparatus of the little group of *Characeæ* presents us with a closer approximation than we have as yet seen among the ordinary Algæ, to that of the higher Cryptogamia, and even, in some particulars to that of Flowering Plants; and this notwithstanding that the Nutritive organs are as simple in their character as are those of Confervæ. The generative apparatus consists of two sets of bodies, both of which grow at the bases of the branches (Fig. 199, B); one set (*b*) is known by the designation of 'globules,' and the other (*a*) by that of 'nucules.'—The 'globules,' which are nearly spherical, have an envelope made up of eight triangular valves, often curiously marked, which enclose a 'nucleus' of a light reddish colour. This nucleus (C) is principally composed of a mass of filaments, rolled-up compactly together; and each of these filaments (D) is formed, like a Conferva, of a linear succession of cells. In every one of these cells there is seen, at the period of maturity of the organ, a spiral thread of two or three coils, (E), which, at first motionless, after a time begins to move and revolve within the cell; and at last the cell-wall gives way, and the spiral thread makes its way out, partially straightens itself, and moves actively through the water for some time, in a tolerably determinate direction, by the lashing action of two long and very delicate filaments, with which these bodies, like the 'antherozoids' of the Fucaceæ, are furnished.—The germ-cell is contained within the 'nucule;' the exterior

of which body is formed by five spirally-twisted tubes, that give to it a very peculiar aspect. What is the precise nature of its nucleus, is as yet uncertain; it would seem probable that this chiefly consists of a mass of starchy matter (resembling that of the 'albumen' of a true seed) in which a single germ-cell is imbedded. For when the nucule is cut across, or is ruptured by pressure, a multitude of little grains are forced out, which are proved by the iodine-test to consist of starch; and it has been determined by the observations of Vaucher, that only one embryo is developed from each nucule, and this by a process that much resembles the germination of a Phanerogamic Plant.*—The *Characeæ* may be multiplied by artificial

Fig. 199.



A, *Chara fœtida:*—B, its fructification; *a*, nucule; *b*, globule:—C, globule laid open:—D, one of its contained antheridial tubes:—E, discharged antherozoids.

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* It is somewhat remarkable that, although the *Characeæ* have long been favourite subjects for observation amongst Microscopists, much should still remain to be determined respecting the structure of the nucule, and the mode in which the generative act is accomplished. The 'antherozoids' were first seen by Bischoff in 1828; but were regarded by him as independent Infusoria. Their exit from the antheridial filaments was first discovered by Mr. Varley, who described them in the "Transactions of the Society of Arts" for 1834; they were afterwards independently discovered by M. Thuret, and described by

subdivision, the separated parts continuing to vegetate under favourable circumstances, and developing the entire structure; and under particular conditions, they develope 'bulbels,' or *gemmæ* of a peculiar kind, being little clusters of cells filled with starch, which sprout from the side of the central axis, and then, falling off, evolve the long tubiform cells characteristic of this group.[*]

488. Although the existence of a true Generative process in *Lichens* cannot be yet said to have been completely established by observation, yet there seems every probability that here, as elsewhere, the concurrence of 'sperm-cells' and 'germ cells' is requisite, and that these are respectively developed within separate organs, which usually coexist, however, in the same plants; that which has long been known as the 'fructification' of the Lichens, being in reality, only the female portion of the apparatus. From the researches of M. Tulasne,[†] it appears that Lichens nearly always possess, in addition to the 'fructification' which is commonly recognised by its projection from the thallus (Figs. 16, 17, 200, A, B, *a a*), a set of peculiar organs of much smaller size (Fig. 200, A, B, *s s*) commonly imbedded in the substance of the thallus, to which he has given the distinctive appellation of *spermogonia*.[‡] These 'spermogonia,' when traversed by a section (D), are found to be cavities lined with a filamentous tissue, whose component filaments are sometimes simple, sometimes ramose; and from the exterior of the cells of these filaments (E), a vast number of minute ovoid bodies are (so to speak) budded-off. These bodies, termed *spermatia* by M. Tulasne, drop when mature from the filaments on which they have pullulated, and escape in great numbers by the orifice of the spermogonium; like the antherozoids of *Florideæ*, they are destitute of any power of spontaneous movement; and as their participation in the production of fertile spores has not yet been demonstrated, we cannot yet indubitably assign to them the character of 'sperm-cells,' although their possession of this attribute is rendered highly probable by the considerations adduced by M. Tulasne.[§]—The female portion of the generative apparatus, though sometimes dispersed through the thallus, is usually collected into special aggregations, which form projections of various shapes; these, although they have received a variety of designations according to their particular conformation, may all be included under the general term *apothecia* (Fig. 200, A, B, *a*, *a*). When these bodies are divided by a vertical section (C) they are found to contain, at their maturity, a number of *asci*, or spore-cases, arranged vertically in the midst of a mass of straight elongated cells or filaments, which are termed 'paraphyses.' Each of

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him in the "Ann. des Sci. Nat." for 1840. The precise relation of the 'nucule' to the 'archegonium' (pistillidium) of higher Cryptogamia, is still a matter of discussion.—See a Memoir by Braun, translated in the "Ann. of Nat. Hist.," 2nd Ser., Vol. XII., p. 297.

[*] The multiplication by bulbels was described by Amici in 1827; but his observations seem to have been forgotten by Botanists, until the fact was re-discovered by M. Montagne ("Ann. des Sci. Nat.," 3e Sér., Botan., Tom XVIII., p. 65).

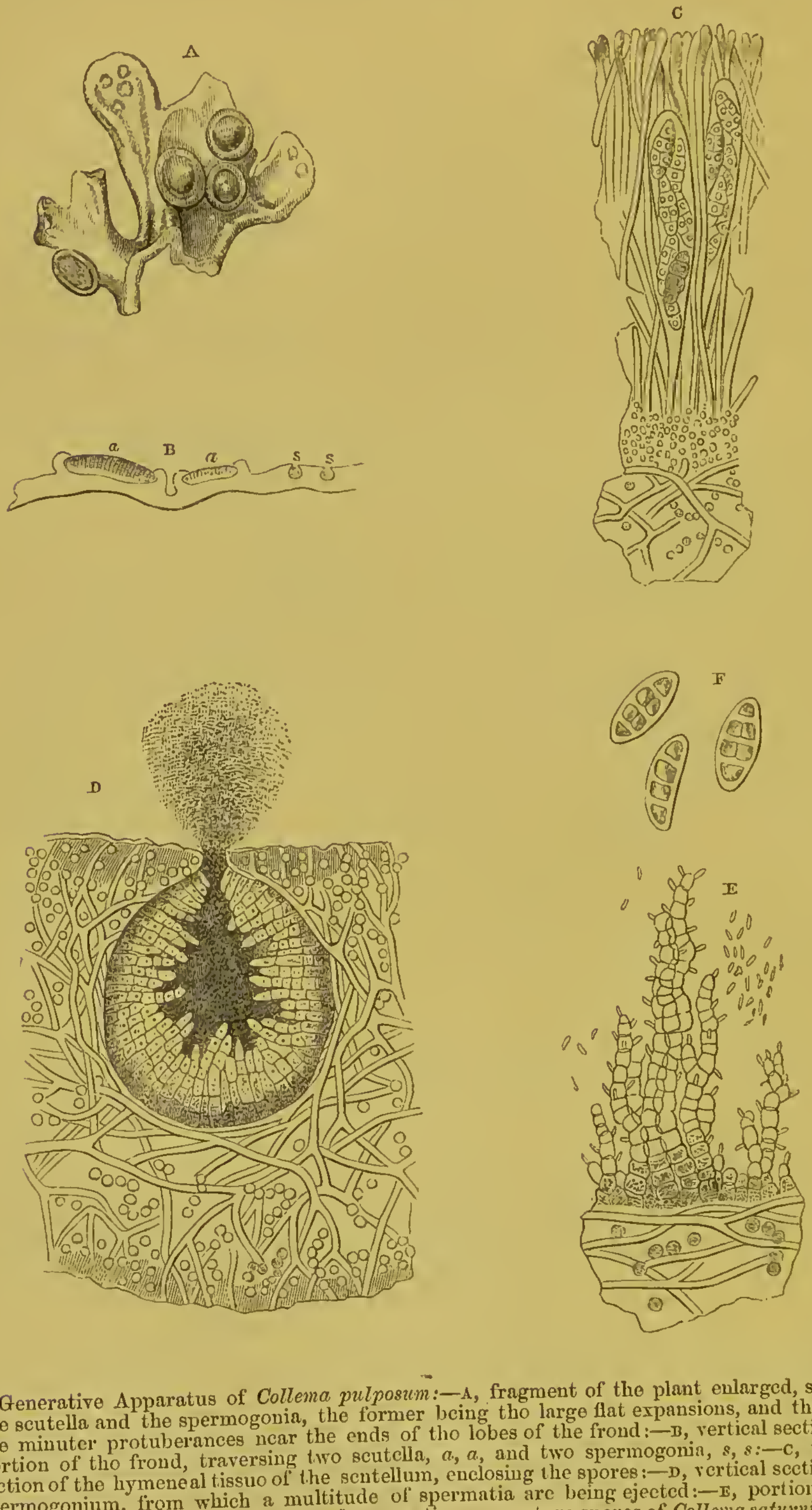
[†] "Ann des Sci. Nat.," 3e Sér., Botan., Tom. XVII.

[‡] The peculiarities of these bodies and of their products, are considered by M. Tulasne as sufficing to distinguish them from the 'antheridia' and 'antherozoids' of higher Cryptogamia, although their functions may be essentially the same.

[§] It does not seem at all improbable that these *spermatia* hold much the same relation to the ordinary antherozoids, that the seminal particles of some of the Entozoa do to the ordinary spermatozoa; being, in fact, the secondary sperm-cells themselves, instead of being filaments developed within those sperm-cells.

the asci contains a certain number of 'spores' (varying from four to sixteen, but being always a multiple of two), which is constant for each

FIG. 200.

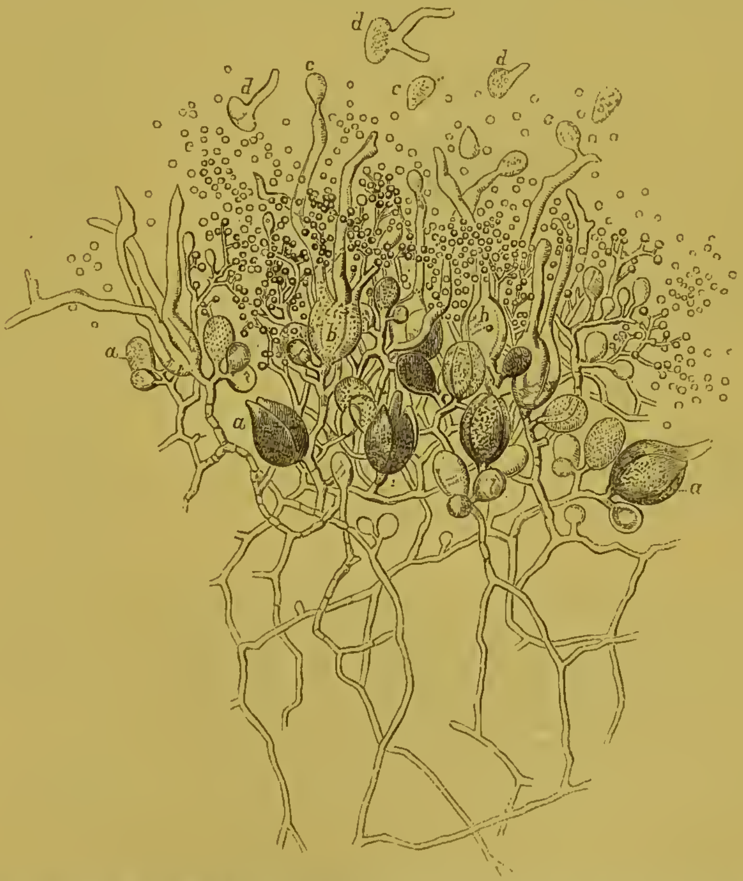


Generative Apparatus of *Collema pulposum*:—A, fragment of the plant enlarged, showing the scutella and the spermogonia, the former being the large flat expansions, and the latter the minuter protuberances near the ends of the lobes of the frond:—B, vertical section of a portion of the frond, traversing two scutella, *a*, *a*, and two spermogonia, *s*, *s*:—C, vertical section of the hymeneal tissue of the scutellum, enclosing the spores:—D, vertical section of a spermogonium, from which a multitude of spermatia are being ejected:—E, portion of the tissue lining this cavity, with detached spermatia:—F, mature spores of *Collema saturninum*.

species; the spores themselves (F) are sometimes multilocular. Each of these spores, when set free from its containing capsule, may give origin, by the usual process of duplicative subdivision, to a new plant. It seems probable, from the analogy of higher Cryptogamia, that every one of the 'asci' originates from a single 'embryo-cell,' which has been developed within a 'germ-cell' as a consequence of the fertilizing influence of the 'spermatoid' bodies evolved from the spermogonia; but nothing certain can as yet be stated on this point.—Lichens multiply also by a method of gemmiparous reproduction, which reminds us of the 'tetraspores' of the *Florideæ* (§ 486); for between their medullary and their upper cortical layers, there is found a layer of rounded green-cells, sometimes nearly continuous, in other cases more interrupted, the cells being aggregated in little masses of variable size, which are termed *gonidia.* These gradually find their way through the cortical layer, so as to appear on the surface as little pulverulent masses, which are termed *soredia*; and, when dispersed and separated, each of the component cells is capable of developing itself into a new 'phytoid.'

489. Our knowledge of the Generative process in *Fungi* is nearly on

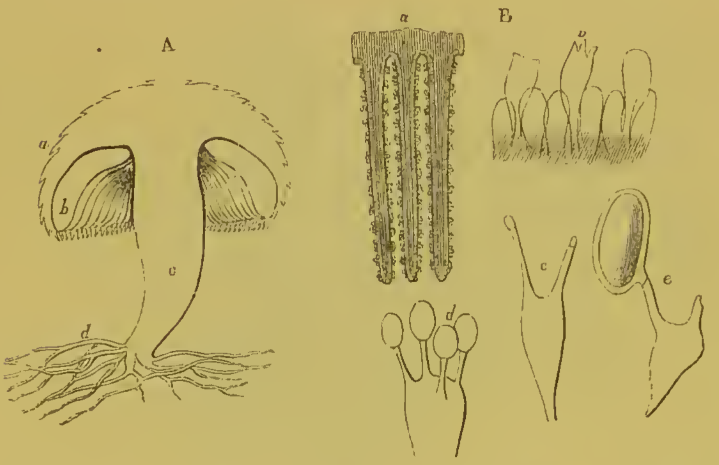
FIG. 201.



Vertical section of the superficial and fertile tissue of *Tremella mesenterica*, showing the basidia, *a*, *a*, in different stages of development; *b*, *b*, the same putting forth sporophores, or elongated filaments bearing spores, *c*, *c*, at their extremities; *d*, *d*, spores in germination; *e*, *e*, the minute globular spermatia, developed at the extremities of special branching filaments.

the same grade with our acquaintance with this function in the Lichens. For although the *reproductive* apparatus of the Fungi is so extraordinarily developed, as to constitute the great bulk of the ostensible plant, yet it is only of late that any evidence has been afforded, by the researches of M. Tulasne,* of the existence of distinct sexes in this group. By the examination of a large number of species belonging to different orders, he has ascertained that the presence of bodies resembling the *spermatia* of Lichens is probably universal in the organs of fructification, at an early period of their development. These bodies (Fig. 201, *e, e*) are budded-off (so to speak) from ramifying filaments, which are sometimes developed in the midst of those that bear the 'spores,' and are sometimes found on other parts of the plant, being occasionally included within distinct conceptacles, or *spermogonia*, as in Lichens.—The ordinary mode in which the 'spores' are developed, is within prolongations from certain cells termed *basidia*, which may be either borne on long filamentous stalks, as in *Tremella* (Fig. 201, *a a*), or may be more compactly clustered together in the substance of a membrane (Fig. 202, B, *a*). These basidia themselves put forth extensions, commonly four in number, which sometimes attain a considerable length (Fig. 201, *b, b*) ; and it is within the extremities of these tubular extensions, according to Schleiden,† that the spores are developed as 'free cells,' which afterwards become detached by the rupture of the basidial filaments.—With a great degree of constancy in these essential features of the structure of the Generative apparatus, this class presents an immense variety in the forms of the organs which contain the spores. The highest type is generally considered to be that of the *Hymenomycetous* group, of which the *Agarics* are characteristic examples. In these, when the fructification is fully developed, we see a dome-shaped body, termed the *pileus* (Fig. 202 A, *a*), surmounted upon a *stipes* or stem (*c*), which rises from the *mycelium* (*d*), that constitutes the nutritive portion of the fabric. The pileus is composed of two membranes, of which the upper and outer is simple and

FIG. 202.



Structure of *Agaricus campestris*:—A, vertical section of the entire plant; showing *a*, the pileus; *b*, the lamellæ covered by the hymenium; *c*, the stipes; *d*, the mycelium:—B, portions of the fructification enlarged; *a*, section through the lamellæ, showing the investing hymenium, and the spores clustered upon it; *b*, portion of hymenium with basidia in four different stages of formation; *e*, basidium somewhat more developed, one of the processes showing the spore in its first stage, the other more advanced; *d*, basidium with four processes and as many half-developed spores; *e*, the upper part of a basidium with a fully-developed spore on one of its processes.

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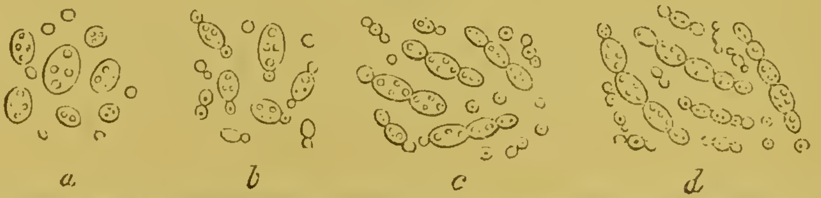
* "Ann. des Sci. Nat.," 3e Sér. Botan., Tom. XIX., p. 193, Tom. XX., p. 129.

† "Principles of Scientific Botany," translated by Dr. Lankester, pp. 153—155.

sterile, like the cortical layer of the Lichens; whilst the inner and lower, which is termed the *hymenium*, contains the basidia. The surface of this membrane is usually extended by duplication or involution; thus in the *Agarics* it forms vertical plates termed *lamellæ* or gills, which radiate from the stipes towards the circumference of the pilcus (A *b*, and B *a*); in *Boletus* and *Polyporus* it lines a mass of vertical tubes arranged like the cells of a honeycomb; and in *Hydnum* it covers the exterior of a similarly-arranged series of solid columns. Of the time at which the act of fecundation is performed, and of the mode in which it is effected, we have as yet no knowledge.—It has long been known that from the same *mycelium*, very different forms of fructification (constituting in this group the ostensible Plants) might be evolved; and it has been recently shown by M. Tulasne, who has added greatly to our knowledge of these, that even the *Thecasporeæ* (which, on account of their bearing distinct spore-cases or thecæ resembling the asci of Lichens, have been regarded as a very distinct group, and have even been referred by Schleiden to the class of Lichens), are *basidiosporous* at one period of their evolution. It may be reasonably suspected that some of these forms of fructification are rather destined for the multiplication of the plant by *gemmæ*, than for the evolution of true generative products.

490. The usual mode of the evolution of the new plant from the spores detached from the parent seems to be, in the first place, the protrusion of one or more long tubes formed by the inner coat, through apertures or fissures in the outer coat. These tubiform cells branch and subdivide, so as to form the *mycelium* or vegetative thallus, which seems common to nearly all Fungi (§ 26). In the *Uredineæ*, however, and perhaps in some other groups, the first product of the germination of the spores is a *promycelium*, which buds-off vesicles that form the true mycelium, and then itself ceases to exist.*—In their early stage of development, it would seem as if these plants could multiply indefinitely by the separation of their component cells. This has been especially noticed in regard to the *Torula cerevisiæ* or 'yeast-plant,' which is found in Yeast in the condition of isolated cells (Fig. 203 *a*); constituting, in fact, a type of vegetation closely analogous to that of the simplest Protophyta. When placed in a fermentible fluid, these cells rapidly multiply; not, however, by that process of duplicative subdivision which prevails among the lower Algæ, but by the budding-forth of young cells from their parietes (*b*). These, in the course of a short time, become complete cells, and again perform the same process (*c*); and in this way, the single cells

FIG. 203.



Different stages of the vegetation of *Torula Cerevisiæ*, or Yeast Plant;—*a*, single cells of which it at first consists; *b*, cells with buds; *c*, the same more advanced; *d*, rows of cells produced by continuance of the budding process.

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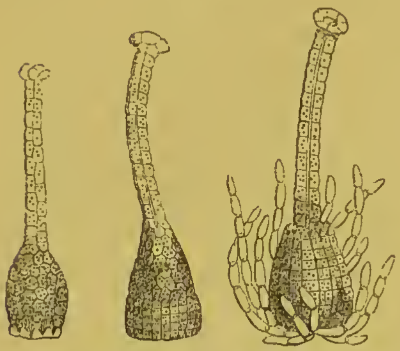
* See Tulasne, in "Comptes Rendus," June 20, 1853.

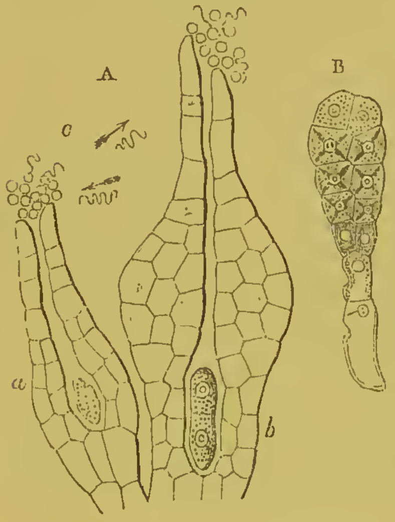
of yeast develope themselves in the course of a few hours, into rows of four, five, or six, which remain in continuity with each other while the plant is still growing, but which separate if the fermenting process be checked, and return to the condition of those which originally constituted the yeast. Thus it is that the quantity of yeast first introduced into the fermentible fluid, is increased by many times during the process. If the process of fermentation be allowed to continue, however, each of the necklace-like filaments extends itself by the production of new cells in continuity with the preceding; and the fructification characteristic of the species is at last evolved.

FIG. 204.



Successive stages of *Archegonia* (pistillidia) of *Marchantia polymorpha.*

FIG. 205.



A, female generative organs of *Jungermannia bicuspidata:*—*a*, unimpregnated archegonium, containing germ-cell; *b*, archegonium, containing fertilized embryo-cell becoming double by subdivision; *c*, spermatic filaments contained within the perianth enclosing the archegonium, and moving in the directions indicated by the arrows:—B, more advanced embryo, from the interior of an older archegonium.

491. In the *Hepaticæ* and *Mosses*, we have no difficulty in recognizing two distinct sets of sexual organs, besides a provision for the production and detachment of free gemmæ or 'bulbels.' The *antheridia*,—which are sometimes buried in the substance of the frond, but in the higher forms project as stalked bodies from its surface (Fig. 23),—contain sperm-cells, within which are developed 'antherozoids,' that closely approximate in appearance and in the nature of their movements to those of the Characeæ. The *archegonia* (or *pistillidia*),* are usually minute flask-shaped bodies (Fig. 204), which, like the antheridia, are imbedded in the substance of the frond among the lower tribes, but project above it in the higher, several being very commonly included within one 'involucrum:' at first they are solid, but the partitions between the interior cells subsequently disappear, and a canal is thus formed (Fig. 205, A *a*), leading to a space at the lower part, within which a free cell is evolved. It is by a process of subsequent development from the archegonia, that those 'capsules' containing 'spores' (Figs. 24, 25, 206) are evolved, which are commonly regarded as constituting the proper 'fructification' of these tribes of Plants. And there is every reason for the belief, that this developmental process originates in a true generative act; the 'germ-cell' within the archegonium being fertilized by the 'antherozoids,' and the 'primordial cell' resulting from this operation evolving itself by

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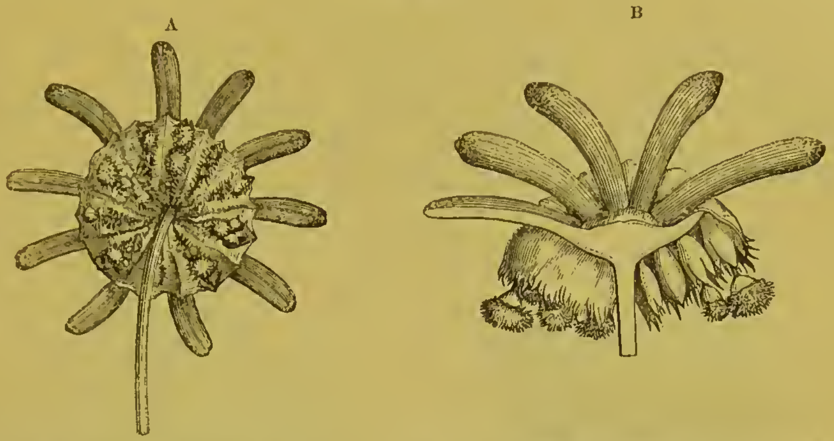
* The term 'pistillidium' is objectionable, as implying a homology with the 'pistil' of Phanerogamia, which does not exist. For whilst the pistil contains *ovules*, the archegonium contains but a single 'germ-cell,' and is itself, perhaps, to be likened to the ovule containing the embryonic vesicle (§ 505).

duplicative subdivision (Fig. 205, A *b*, B) into the spore-capsule or fruit (§ 27). For the antherozoids have been often observed by Hofmeister swimming about around the archegonia within their involucrum; and it has been ascertained that when the antheridia and archegonia are developed upon different individuals, as happens in some species of Mosses, the evolution of the latter into capsules does not take place, unless the plants bearing the former are in the neighbourhood. Moreover, it has been shewn by Mr. Valentin's elaborate investigations,* that no impregnation of the contents of the capsule, by the introduction of any external substance into its cavity, can take place *after* the formation of the spores. In this point of view, such a mass would represent the clustered spores of the Fuci (§ 485) in every respect, save that the process of subdivision has proceeded much further; it would also represent the single embryo of the Flowering-plant, which also is composed of a mass of cells originating in the subdivision of the primordial embryo-cell. The 'spores,' however, are capable of existing independently of each other, like the cells of a Palmella; and thus from each of them a distinct 'phytoid' may arise.—In the development of one of these cells into a new plant, the first stage is the rupture of its outer coat, and the protrusion of the delicate cell-wall that lined it. By the subdivision of this primary cell, an embryonic cluster is soon formed, presenting a very confervoid aspect, so as closely to resemble the mature condition of plants much lower in the scale of organisation. It is by a continuation of the same process, that the 'frond' of the *Hepaticæ*, which presents various gradations from a simple and almost amorphous expansion to an assemblage of parts arranged with some degree of regularity upon an axis, is gradually evolved; and from every part of its under surface proceed radical fibres, which remain in the condition of the simple confervoid filaments first put forth. But in *Mosses*, in which there is a more perfect separation of the axis and its foliaceous appendages, we find the stem gradually developed from one end of the primitive confervoid body or *prothallium*, at first, however, as a mere homogeneous mass of cells; the leaves are

FIG. 206.



Inferior aspect, A, and sectional view, B, of one of the lobed receptacles of *Marchantia polymorpha*, showing the sporangia on its under surface.

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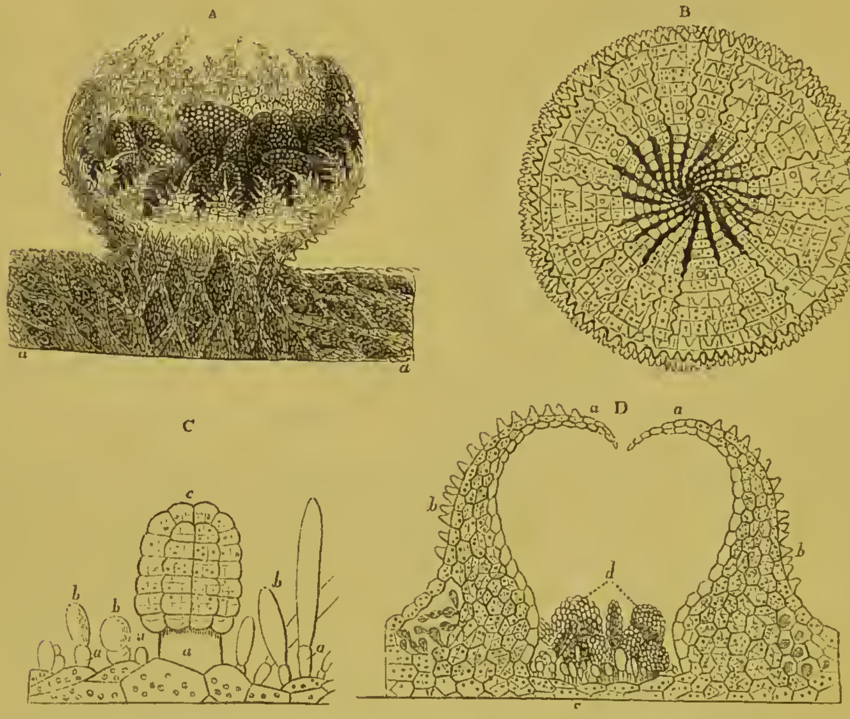
* "Linnæan Transactions," Vol. XVII.

then put-forth from the axis, one after another; and the structure characteristic of the perfect organs becomes progressively apparent. No true root, or descending axis, is ever evolved in Mosses; and the radical filaments, which proceed from the base of the stem, remain in the simple condition of those which are put forth from the prothallium.*

492. In both these tribes of Cryptogamia, there is a provision for the multiplication of independent 'phytoids' by gemmation; and this provision is peculiarly elaborate in *Marchantia*. On various parts of the surface of its thallus, there may very commonly be found little basket-like conceptacles (Fig. 207, A, B) in different stages of growth; and within these are a number of discoidal bodies, each composed, when fully developed, of two or more layers of cells. These gemmæ are at first evolved as single globular cells, supported upon footstalks which consist of single elongated cells, rising from the base of the conceptacle (C, D); the single cells, undergoing multiplication by duplicative subdivision, are developed into the disks; and these, when mature, spontaneously detach themselves from their pedicels, and lie free within the cavity of their con-

Fig. 207.



Gemmiparous conceptacles of *Marchantia polymorpha*:—A, conceptacle fully expanded, rising from the surface of the frond *a a*, and containing disks already detached:—B, first appearance of the conceptacle on the surface of the frond, showing the manner in which its fringe is formed by the splitting of the cuticle:—D, section of a conceptacle in progress of expansion, showing *a*, *a*, its thin fringed edges, *b*, *b*, the thicker walls of its lower portion, and *c* its base whence spring *d* the bulbels:—C, portion of the base more enlarged, showing the bulbels in various stages of development; *a*, pedicel, *b*, *b*, bulbels in their earliest condition, *c*, bulbel more advanced.

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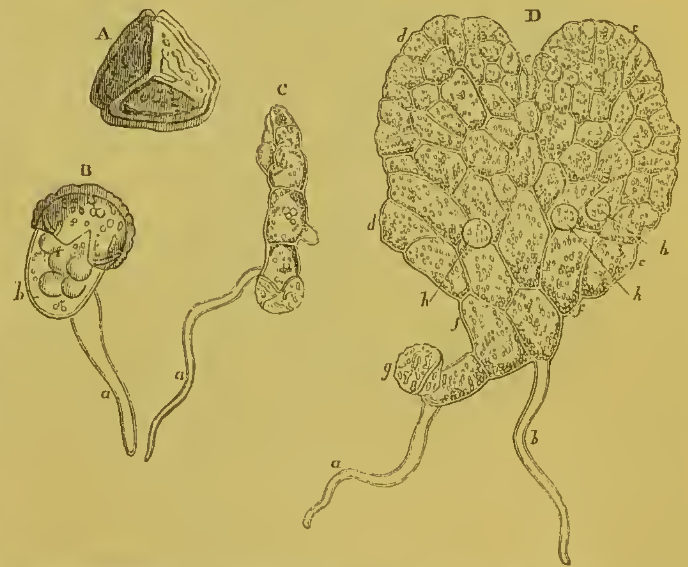
* This view of the generative process in Mosses, first put forth (1848) by Mr. G. H. K. Thwaites ("Ann. of Nat. Hist.," 2nd Ser., Vol. I., p. 105), has since been confirmed by the researches of Hofmeister ("Vergleichende Untersuchungen der Keimung, Entfaltung und Fruchtbildung höherer Kryptogamen," &c., 1851).

ceptacle. Most commonly they are at last washed-out by rain, and are thus carried to different parts of the neighbouring soil, on which they grow very rapidly when well supplied with moisture; sometimes, however, they may be found growing whilst still contained within the conceptacle, and seem to graft themselves (as it were) on the stock from which they are developed.—Among *Mosses*, again, there are several instances in which buds that spontaneously detach themselves, or 'free gemmæ,' are developed, sometimes from the stem, sometimes from the leaves, and sometimes from the root-fibres; and this kind of multiplication may even take place in the confervoid state of the 'prothallium,' which frequently separates into several parts, from each of which a new 'phytoid' may be evolved. There are certain species of Mosses, which rarely, if ever, occur with true fructification in certain localities, their propagation being effected almost solely by the spontaneous detachment of gemmæ which are put-forth from their stems; and thus among these humble plants, the product of a single sexual operation may attain the age of our largest trees, and may occupy as large a space in the economy of nature.*

493. It was by the discoveries made not long since in regard to the processes of Generation and Development in the class of *Ferns*, that a new light was first thrown upon the nature of these operations, not only in this particular group, but in the Cryptogamia in general. It now appears that what had been previously considered the 'fructification' of the Fern,—namely, the collections of *thecæ* containing *spores*, usually found on the under sides or at the edges of the fronds (Fig. 27),—is really an apparatus for gemmiparous production; the 'spore' not being the immediate product of the sexual or true generative operation, but being a free *gemma*, which, when cast-off by its parent, forthwith developes itself into a structure containing sexual organs, from which the new generation really originates. It will be convenient, however, in describing the process of evolution, to commence with the 'spore,' as the best-defined starting-point. This body is a *cell* of irregular form, but usually somewhat pyramidal (Fig. 208, A);

FIG. 208.



Development of Prothallium of *Pteris serrulata*;—A, spore set free from the theca:—B, spore beginning to germinate, putting-forth the tubular prolongation *a*, from the principal cell *b*;—C, linear series of cells, formed by the multiplication of the original:—D, prothallium taking the form of a leaf-like expansion; *a*, first, and *b*, second radical fibre; *c*, *d*, the two lobes, and *e* the indentation between them; *f f*, under part of the prothallium; *g*, external coat of the original spore; *h*, *h*, antheridia.

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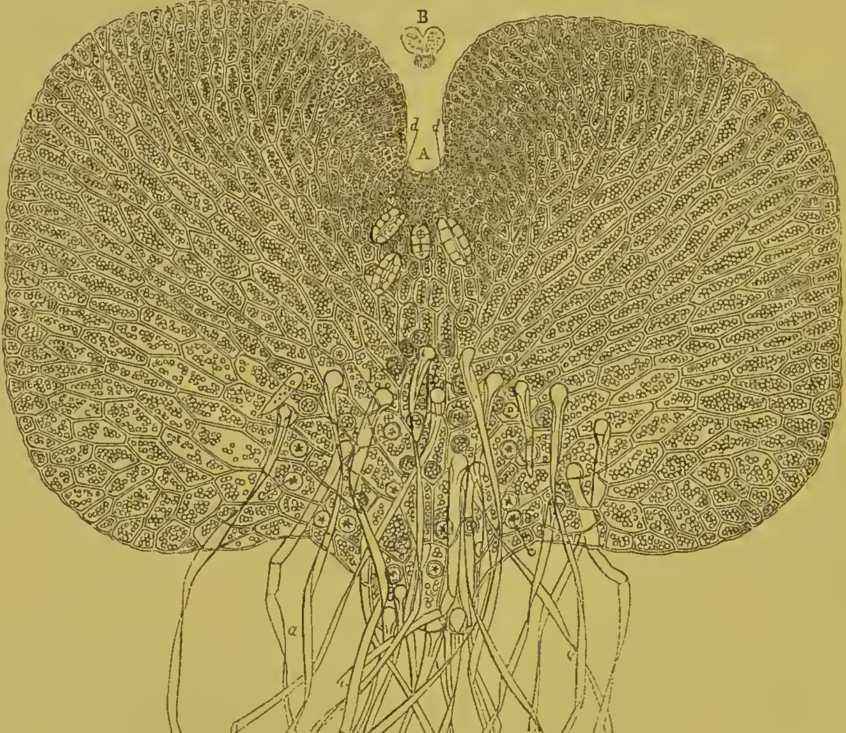
* Thwaites, Op. cit., Vol. II., p. 314.

its outer wall is formed of a brownish-coloured resisting membrane, in some part of which is a minute aperture; its inner wall is extremely thin and transparent; and the cavity of the cell contains an oleaginous mucilage, in which are usually found three nuclei. Under the influence of warmth, moisture, and light, the spore begins to enlarge, the first indication of its increase being the rounding-off of its angles; then from the orifice in its outer wall is put-forth a tubular prolongation of the internal cell-wall (*a*), which serves as a radical fibre, absorbing nourishment from the surface on which the spore is lying; and by this absorption, the inner cell is so distended, that it bursts the external unyielding integument, and is now directly exposed to the influence of light (B). Its contents speedily become green; and the cell itself elongates in a direction opposite to that of the root-fibre, so that it acquires a cylindrical form. A production of new cells then takes place from its extremity; and this at first proceeds in a single series, so as to form a kind of confervoid filament (C); but the new growth soon takes place laterally as well as longitudinally, so that a flattened, leaf-like expansion or 'thallus,' closely resembling that of a young Marchantia, is soon formed. This thallus varies in its configuration in different species of Ferns; in the species here figured (D), it is bilobed, the two divisions (*c*, *d*) being separated by a kind of notch (*e*); but its essential structure

FIG. 209.

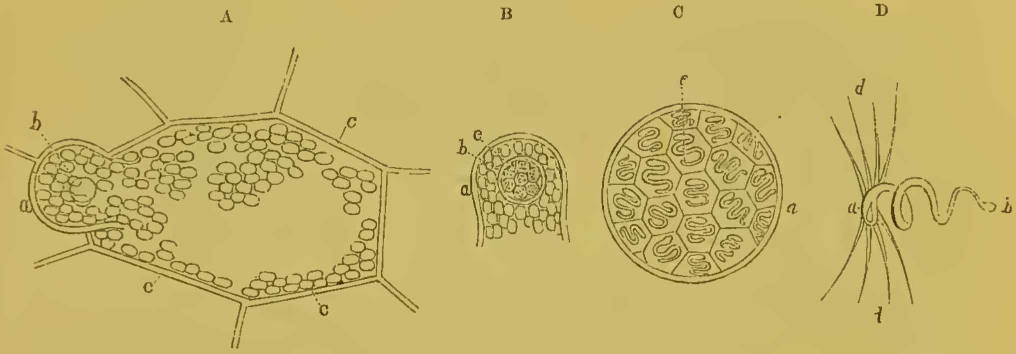


More advanced Prothallium of *Pteris serrulata;* B, natural size; A, magnified;—*a a*, root-fibres; *b*, antheridia; *c*, the same after the discharge of their contents; *d*, pistillidia.

is always the same. From its under surface are developed additional root-fibres, which serve to fix it in the soil, and, at the same time, to supply it with moisture.—To this body, which, in its fully developed form, is represented in Fig. 209, the name of *prothallium* has been appropriately given.*

494. At an early period in the development of the 'prothallium,' certain peculiar glandular-looking bodies are seen projecting from its under surface (Fig. 208, D, *h*, *h*); these augment in number with the advance in growth; and at the time of the complete evolution of the 'prothallium,' they are seen in considerable numbers (Fig. 209, A, *b*, *c*), especially about its base, near the origins of the radical fibres (*a*, *a*). These bodies owe their origin to a peculiar protrusion which takes place from certain of the cells of the 'prothallium' (Fig. 210, A, *a*); this is at first entirely filled with chlorophyll; but soon a peculiar free cell (*b*) is seen in its interior, filled with mucilage and colourless granules. This cell gradually becomes filled with another brood of young cells (B, *e*); it increases considerably in its dimensions, so as to fill the projection which incloses it; this part of the original cavity is now completely cut-off from the primary-cell, of which it was an offshoot; and the *antheridium* (as this peculiar cell with its contents is now to be called) henceforth ranks as a distinct and independent organ. Each of the secondary cells contained within the primary cell of the 'antheridium' is seen, towards the period of maturity, to contain a spirally-coiled filament (C); and when these cells have been set free by the bursting of the antheridium (Fig. 209, A, *c*), they themselves burst and give exit to their 'antherozoids,' which execute rapid movements

FIG. 210.



Development of the *Antheridia*, and *Antherozoids*;—A, one of the cells of the prothallium, bounded by the cell-wall *c c c*, giving off a projection at *a*, which contains a peculiar secondary cell, *b*;—B, further development of this part; *a*, projection of the primary-cell; *b*, secondary cell or antheridium filled with a new generation of cells *e*;—C, antheridium completely developed and shown on a larger scale; *a*, wall of the secondary cell; *e*, contained cells; each inclosing a spiral filament;—D, one of the spiral filaments (antherozoids) highly magnified; *a*, large extremity; *b*, other extremity, less dilated; *c*, cilia.

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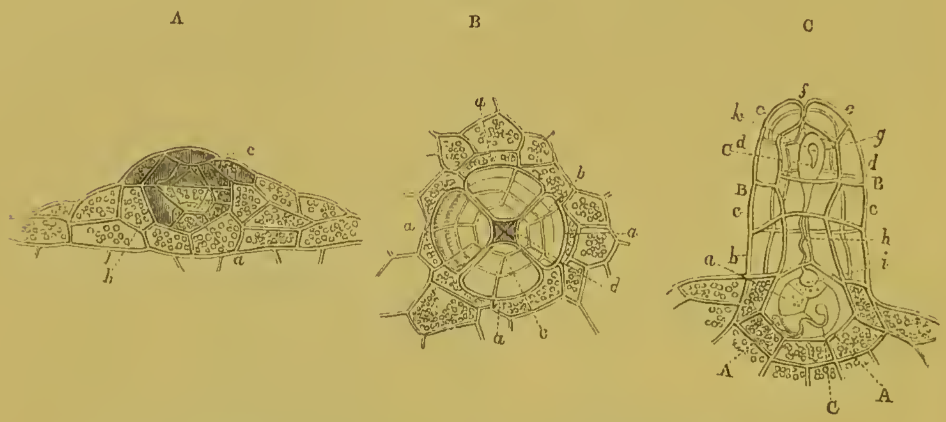
* This "Marchantia-like expansion" has been long known as the first production from the spore; and was described in the earlier editions of this work as a *cotyledon* developed for the elaboration of nourishment for the young Fern which is afterwards to sprout from its centre. It will be seen hereafter, that though it undoubtedly performs an *analogous* function, yet that it cannot be regarded as *homologous* with a cotyledon; its relation to the young Fern being that of a parent to its offspring, and not that of a temporary leaf to a more permanent one.

of rotation on their axes, partly dependent upon the long cilia with which they are furnished (Fig. 210, D). Each of these spiral filaments makes from two to three turns; its anterior extremity (*a*) is considerably enlarged, and seems to contain a minute vesicle; its posterior extremity (*b*) is also somewhat dilated.*

495. Besides these bodies, the 'prothallium' bears a small number of others, differing essentially from the preceding in character, and usually occupying a different position; thus in the bilobed frond of *Pteris serrulata*, they are seen near the median indentation (Fig. 209, *d*, *d*). The number of these bodies seems indeterminate; sometimes only three, in other instances as many as eight or more, being seen in prothallia of the same species. Each of them at its origin presents itself only as a slight elevation of the cellular layer of the prothallium, within which is a large intercellular space, containing a peculiar cell (Fig. 211, A, *a*), and opening externally by an orifice (*c*) at the summit of the projection; but when fully developed, it is composed of from ten to twelve cells, built-up in layers of four cells each, one upon another (B), so as to form a kind of column (C), having a central canal which leads down to the cavity at its base. The subsequent history of this body shows that it is to be considered as an *archegonium* or female organ; and that the peculiar cell contained in the cavity at its base is to be regarded as a 'germ-cell' or 'embryonal vesicle.' As the development of the archegonium is taking place, it appears that certain of the spiral filaments or 'antherozoids,' set

Fig. 211.



Development of the *Archegonium* (pistillidium) of *Pteris serrulata*;—A, side view in its early state; *a*, germ-cell; *b*, cells of the archegonium; *c*, opening at the summit;—B, archegonium in more advanced stage, seen from above; *a a a a*, cells surrounding the base of the cavity; *b*, *c*, *d*, successive layers of cells, the highest enclosing a quadrangular orifice;—C, vertical section at the time of impregnation; A A, cavity containing the germ-cell; B B, walls of the archegonium, made up of the four layers of cells, *b*, *c*, *d*, *e*, and having an opening on the summit at *f*; C C, spiral filaments; *g*, large extremity, enclosing antherozoid, *k*; its thread-like portion *h* lying in the canal of the archegonium, and its small end *i* dilated into a globular form, and in contact with the germ-cell.

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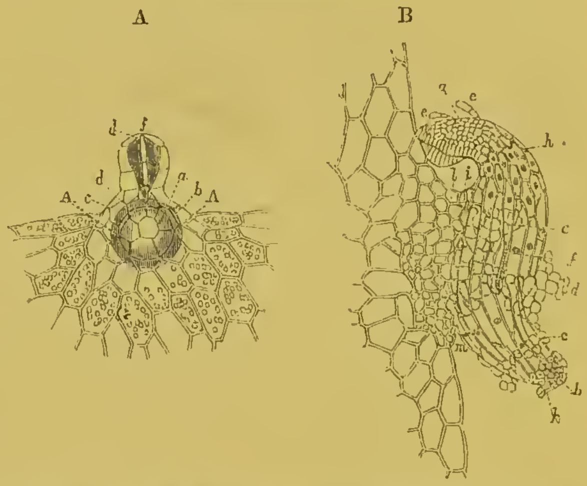
* The discovery of these antheridia in the 'pro-embryo' of Ferns was first made by M. Naegeli in 1846. He gave an accurate account of the production of the spiral filaments, but entirely overlooked the 'archegonia' (presently to be described), which he seems to have regarded as antheridia in a different grade of development.

free from the antheridia, penetrate into its cavity; and that one of these comes into peculiar relation with the embryonal vesicle by its smaller extremity (C, *i*), which dilates into a globular form, and becomes detached from the remainder of the filament. The whole of the filament, as it lies in the canal of the archegonium, is seen to have enlarged considerably, probably by the absorption of mucus whilst it traverses the under-side of the prothallium. The contact of the dilated end of the 'antherozoid' with the 'germ-cell,' or embryonal vesicle, appears to constitute an act of fecundation, precisely equivalent in all essential particulars to the 'conjugation' of the Protophyta; and as the result of this fecundation, a new body, the primordial cell of the true embryo, makes its appearance in the interior of the embryonal vesicle.

496. The germ has at first a globular form, and consists of a homogeneous mass of minute cells (Fig. 212, A, *a*), formed by the subdivision of the primordial embryo-cell; but as its development proceeds, rudiments of special organs begin to make their appearance; it grows at the expense of the nutriment prepared for it by the 'prothallium;' and it soon bursts forth from the cavity of the archegonium, which organ, in the meantime, is becoming atrophied. In the very beginning of its development, the tendency is seen in the cells of one extremity to grow upwards, to form the stem and leaves; and in those of the other extremity to grow downwards, to form the root. The condition of the embryo when these parts are first distinctly evolving themselves, and its relation to the prothallium, are shown in Fig. 212, B; in which we see the rudiment of the first leaf at *a*, some of the hairs upon its surface at *e*, the first cells of the leaf-stalk at *h*, those of the terminal bud or 'growing-point' of the stem at *i*, those of the root at *b*, those of the prothallium at *l m*, and the fragments of the archegonium at *c c* and *d*. Already spiral vessels begin to show themselves, as at *f*.—The further progress of this germination may be readily apprehended. When the true root has been sufficiently evolved to serve for the absorption of fluid nutriment, and the first true frond has been expanded to the air, so that the young plant can elaborate its own alimentary materials, the prothallium, whose function is now discharged, decays away. The axis, elongating itself upwards to form the stem, gives off successive leaves; and some or all of these, when fully evolved, bear

FIG. 212.



Development of the Embryo of *Polypodium aureum*:—A, archegonium sometime after fertilization, containing the germ-cell A, within which is seen the globular embryonic-mass *a*; at *b*, *c*, *d*, are shown the contracted cells of the archegonium, and at *f* the opening at its summit:—B, embryo much further advanced, and emerging from the archegonium; *a*, leaf; *b*, root; *c c*, *d*, fragments of the archegonium; *e*, hairs; *f*, first spiral vessels; *h*, leaf-stalk; *i*, terminal bud or growing-point; *k*, root-sheath; *l*, *m*, portion of prothallium supporting the embryo.

the *sori*, or clusters of *thecæ*, which produce a new brood of spores.*—Besides this method of multiplication, some Ferns possess another, which corresponds with the formation of free gemmæ in the Marchantia; bulbels being formed from the tissue of the leaves, either on the surface or in the angles of the lobes; and then dropping-off and becoming independent plants.

497. Thus the history of the Fern presents us with a very characteristic example of the so-called "alternation of generations;" and one, too, which remarkably illustrates the general principle which has been already laid-down (§ 478) with regard to the true nature of this alternation. Starting from the spore, we must consider each prothallium as, properly speaking, a distinct 'phytoid' (§ 480); it is completely independent of the plant from which the spore was detached; and it obtains and elaborates its own nutriment. The life of the prothallium terminates, however, with the evolution of the young Fern, which is produced from it by a true process of sexual generation: whilst the Fern, when fully evolved as such, gives origin to a new series of prothallia by the process of sporuliferous gemmation, and dies without having reproduced its kind in any other way. Thus, between each two generations of true Ferns, a prothallium intervenes, springing from the first by gemmation, and giving origin to the second by true sexual reproduction; and in like manner, between each two generations of prothallia, there is a true Fern, originating in the sexual operations of the one, and producing the other by gemmation. Hence in the case before us, we have a complete exemplification of the general fact, that the so-called 'generations' are not related to one another in the same way; but that whilst their relationship is in the one case that of offspring to parent, it is in the other that of offset to stock. The latter cannot be legitimately held to constitute a distinct 'generation,' if that term be used in the signification in which it has until recently been ordinarily understood in physiology,—namely, the production of a new being by sexual union. And if we carefully examine the case before us, we shall see how little claim the prothallium has, to be considered as a 'generation' distinct from that of the Fern which produces the original spore. For let it be supposed that the prothallium, instead of being cast-off from the Fern in the state of spore, had been developed in continuity with it (as we shall find its equivalent to be in the *Coniferæ*, § 501), we

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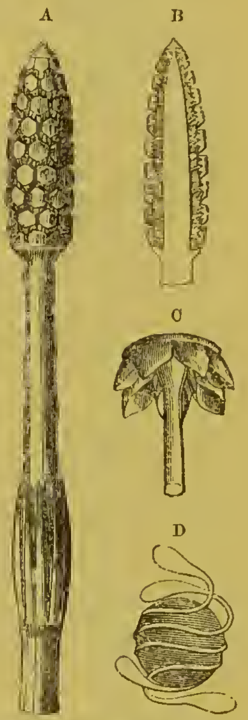
* The discovery of the archegonia and of their contained germ-cells, of the fecundation of these by the spermatic filaments, and of the true relation of the young Fern to the prothallium, is due to Count Leszczyc-Suminski, whose very beautiful Monograph "Zur Entwickelungs-Geschichte der Farrnkräuter," published at Berlin in 1848, also contains a much more elaborate history of the development of the young Fern, than had been previously given. In one point, however, he seems to be undoubtedly in error; viz., in having considered the primordial cell of the embryo to have originated in the dilated extremity of the antherozoid, instead of being a new formation within the germ-cell.—In the Report upon Count Suminski's observations, presented to the Berlin Academy by Dr. Münter, he states that a part of the fertilizing process above described,—namely, the penetration of the moving filaments into the orifice of the archegonium,—has been *repeatedly witnessed* by himself and Prof. Link; but it appeared to them that the antherozoids resolved themselves into "little heaps of mucus" after their motion had ceased. Whichever statement is the true one (and the latter is in very curious accordance with the observations of Mr. Newport upon the fertilization of the ovum of Frogs, § 526), the essence of the matter remains the same; for in either case, the contents of the sperm-cells and those of the germ-cells are brought into mutual relation.

should then have distinctly recognized it as part of the true generative apparatus of the Fern itself, like the flower of the Flowering-plant; the germ being the product of the joint action of the 'sperm-cells' and the 'germ-cells' which both alike contain. That the embryonal vesicle in the Fern lies naked in the cavity of the archegonium, from the walls of which is supplied the nourishment which it imbibes,—whilst in the Phanerogamia it is surrounded with a mass of nutriment prepared and stored-up there before its impregnation,—seems to constitute the most important difference in the conditions under which the germ is developed in the two groups respectively; and this difference, however valuable in a systematic arrangement of Plants, as serving for the separation and definition of these groups, cannot be considered as having any fundamental importance in a physiological point of view. Now as the development of the generative apparatus is necessary to our idea of a perfect 'individual,' we must regard the evolution of the prothallium as really completing the preceding Fern-generation, instead of constituting an entirely new one; unless we are prepared to go so far as to maintain that the mere fact of its detachment gives it a title to the appellation 'new generation,' which would be to extend very widely the usual acceptation of the term.

498. The little group of *Equisetaceæ* seems nearly allied to the Ferns in the type of its Generative apparatus, although that of its vegetative portion is very different; for whilst the development of the *leaf* preponderates in the latter, it is the *stem* with its ramifications which constitutes the chief part of the spore-bearing plant in the former. The fructification forms a sort of cone or spike at the extremity of certain of the branches (Fig. 213, A, B); and consists of a cluster of peltate (shield-like) disks, each of which (C) carries a circle of thecæ or spore-cases, that open by longitudinal slits to set free the spores. Each of these bodies (D) has attached to it a pair of elastic filaments, which are set in motion by the slightest application of moisture; these are formed as spiral fibres on the interior of the wall of the primary cell within which the spore is generated, and are set free by its rupture; and their function is doubtless to assist in the dispersion of the spores. The development of the spores takes place in a manner essentially the same as that of the spores of Ferns, a prothallium being first evolved, and antheridia and archegonia being produced from this; it may be reasonably surmised, therefore, that the process of fecundation is the same, and that the spore-bearing plant which arises from the prothallium is its real generative offspring, instead of being a later phase of its own development.*

Fig. 213.



Fructification of *Equisetum arvense*:—A, spike; B, section of its fertile termination; C, sporangia; D, spore.

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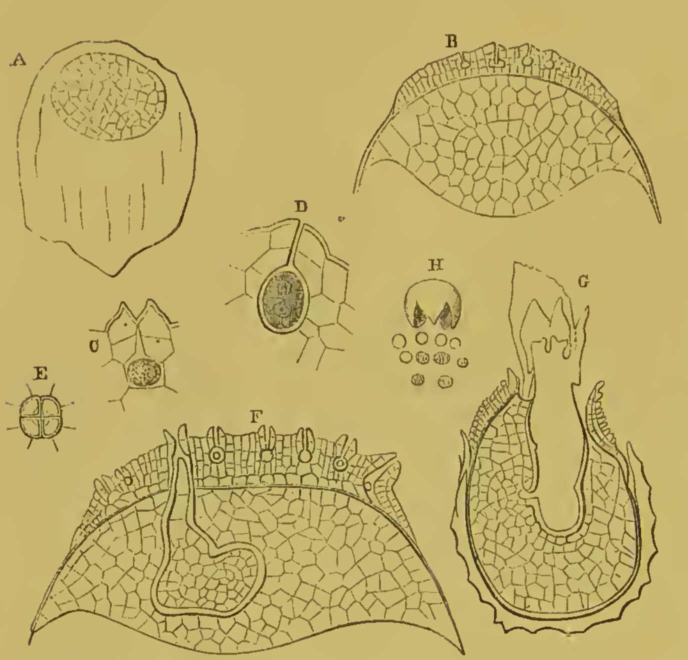
* See Hofmeister, Op. cit., p. 89, *et seq.*; and Thuret, "Ann. des Sci. Nat.," 3e Sér., Botan., Tom. XVI., p. 31.

499. Among certain of the *Lycopodiaceæ,* a marked difference presents itself in the mode in which the Generative act is performed. In *Selaginella* and its allies, two kinds of fructification are found; one consisting of two-valved capsules containing a large number of what are commonly designated as 'small spores,' whilst to the other belong certain bodies termed '*oophoridia,*' each of which produces four 'large spores.' The small spores are really 'sperm-cells;' for each includes a multitude of secondary cells, every one of which contains an 'antherozoid' (Fig. 214, H): hence the capsules from which they are evolved are true antheridia. The 'antherozoids' are not set free, by the rupture of their containing cells, until some time after their emission from the antheridia; and in the mean time, each of the larger spores gives origin to a cellular expansion (A) or prothallium, from which are soon developed archegonia (B) closely resembling those of the Ferns, each having a free embryonal vesicle (C) lying in a cavity to which a passage leads-down from the quadrifid papilla (D) at its summit. It may be presumed that the process of fecundation is the same as in Ferns; for two new cells (D) soon take the place of the original germ-cell; these divide and extend themselves into a cellular mass (F), which is at first imbedded in the substance of the prothallium, but which soon pushes-upwards a bud (G), and at the same time transmits a radicle downwards, bursting through the prothallium, which speedily disappears.—In the *Lycopodium* itself, however, and in some other members of this family, only one kind of spore (apparently most resembling the 'small spore' of Selaginella), has been yet discovered; and it is suggested by Hofmeister (to whom we owe the discovery of the true nature of the generative process in the Selaginella) that the process is here analogous to that which takes place in the Ferns; the spore evolving

FIG. 214.

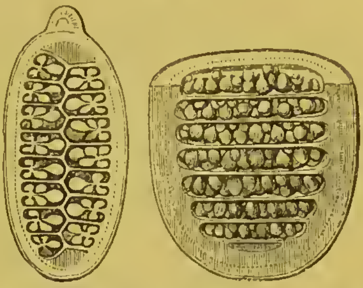


Generation of *Lycopodiaceæ:*—A, interior of large spore of *Selaginella Martensii,* showing the young prothallium at the upper end:—B, vertical section of prothallium and upper half of large spore of *Selaginella denticulata,* showing several archegonia:—C, an archegonium of *S. Martensii,* with its contained germ-cell;—D, archegonium of *S. denticulata* just impregnated, with its embryo-cell dividing into two:—E, an archegonium seen from above:—F, vertical section of prothallium, and upper part of the large spore of *S. denticulata,* in a more advanced stage; the embryo developed from one of the archegonia having become imbedded by downward growth in the cellular tissue filling the upper part of the cavity of the spore:—G, young embryo breaking through the prothallium, and protruding its bud from the spore:—H, small spore (antheridium) of *S. helvetica,* bursting and discharging cellules containing antherozoids.

a prothallium, from which both antheridia and archegonia are put forth.*

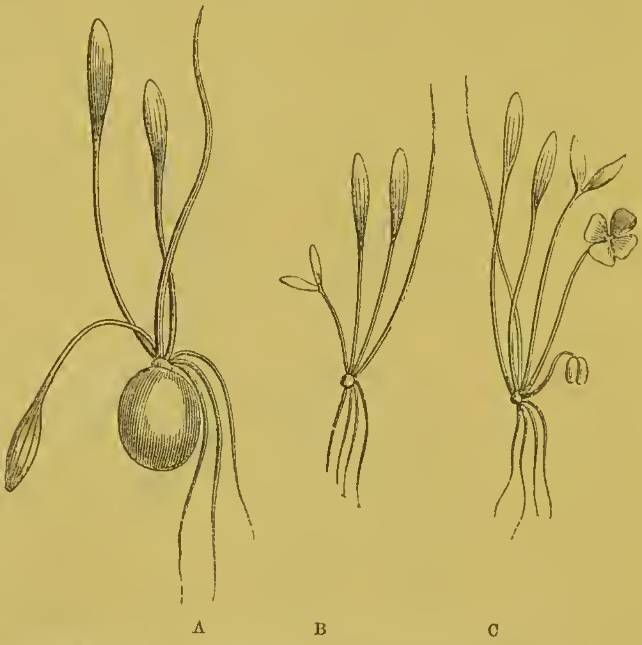
500. The manner in which the Generative function is performed in the little group of *Marsileaceæ* (Rhizocarpeæ) presents so many points of apparent resemblance to that which is characteristic of Phanerogamia, that many Botanists (among them Schleiden) have transferred them from the Cryptogamic to the Phanerogamic division of the Vegetable kingdom. It has been shown by Hofmeister, however, that the generation of these plants corresponds in the most essential particulars with that of Lycopodiaceæ. Their fructification usually consists of two-valved bodies termed *sporocarps;* which, when cut open, are found to include a number of larger and smaller capsules in close approximation (Fig. 215). The smaller capsules are 'antheridia;' for the small spores which they set free on the dehiscence of the fruit, themselves give exit to secondary cells, each containing an 'antherozoid.' On the other hand, the larger capsules are 'oophoridia;' for the 'large spores' which they give out, and which at first contain nothing but starch and oil-globules, gradually become filled with cells constituting a 'prothallium.' From each prothallium, only a single archegonium, with its contained germ-cell is developed; and this projects at an aperture formed by the separation of the spore-coats at that point, its extremity being a quadrifid papilla, down the centre of which the fecundating antherozoid can find its way to the germ-cell within.† The embryo is developed within the germ-cell, as an entirely new formation; and the manner in which it is connected with the 'large-spore' (Fig. 216, A), strongly reminds the observer of the germination of a Phanerogamous plant. The first leaves of a Marsilea that are put-forth, are of very simple form (A); in the next stage (represented on a smaller scale at B), some of the leaves are

FIG. 215.



Vertical and transverse sections of Sporocarp of *Marsilea quadrifolia.*

FIG. 216.



Germination of *Marsilea Fabri*, in three successive stages, A, B, C.

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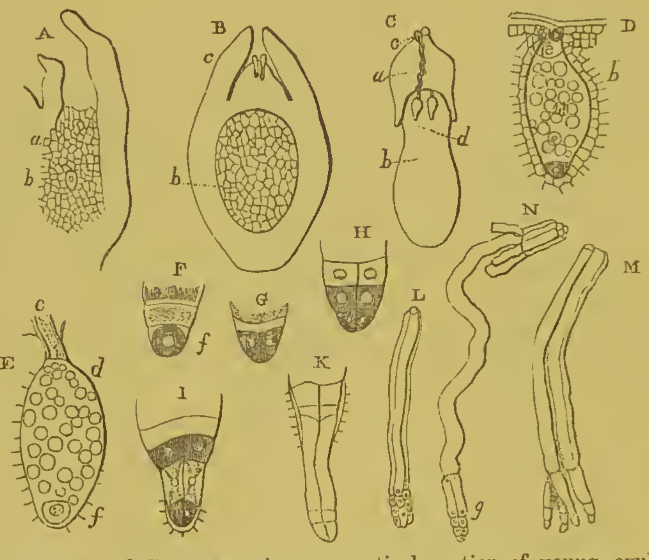
[*] Op. cit., p. 111, *et seq.*

[†] See Hofmeister, Op. cit., p. 103, *et seq.*—The four cells of the archegonium surrounding the central canal were mistaken by Schleiden for pollen-tubes.

bifid; and in a third stage (c), the quadrifid division characteristic of the perfect plant (Fig. 31) begins to show itself.—It has been long since experimentally proved, that germination will not take place from the 'large-spores,' unless the 'small spores' are present; so that the relative sexual nature of the 'antheridia' and the 'archegonia' may be considered to be in this instance beyond reasonable doubt.

501. The recent researches of Hofmeister* upon the *Gymnospermeæ* (Conifers and Cycads), which confirm and extend the results previously obtained by Dr. Robert Brown, show that this group holds a position which is most curiously intermediate between the Lycopodiaceæ and the ordinary (Angiospermous) Phanerogamia. The bodies concerned in the generative process are developed in distinct organs, which, whilst possessing the essential parts of the 'flower' of ordinary Phanerogamia, have no resemblance to it in appearance. The 'sperm-cells' are now evolved as 'pollen-grains' (§ 503), differing essentially from the sperm-cells of Cryptogamia, in the mode in which they impart their fecundative influence to the 'germ-cells;' they are developed, however, not in a proper 'anther,' but in the substance of a body that retains in some degree the leafy type; and an assemblage of such bodies forms the 'catkin.' The (so-called) 'ovules,' on the other hand, are developed from carpellary leaves which do not close-in around them; and it is of an assemblage of

Fig. 217.



Generative Apparatus of *Gymnospermia*:—A, vertical section of young ovule of *Pinus*; *a*, nucleus; *b*, embryo-sac:—B, vertical section of more advanced ovule; *b*, embryo-sac filled with cellular tissue; *c*, pollen-tubes penetrating the nucleus; C, portion of embryo-sac and upper part of the nucleus; *b*, embryo-sac; *c*, pollen-tube traversing the tissue of the nucleus *a*; *d*, corpuscles:—D, vertical section of corpuscle of *Abies*, just ripe for impregnation; *b*, tissue filling embryo-sac; *e*, two of the four cells between which the pollen-tube passes; *d*, free cells in cavity of corpuscle:—E, vertical section of corpuscle of *Pinus*, at which the pollen-tube, *c*, has just arrived; *d*, free cells in cavity of corpuscle; *f*, embryonal vesicle:—F, F, G, I, K, progressive stages of development of suspensors of *Pinus*:—L, suspensor just before separating: —M, the same detached below:—N, a suspensor (three being cut away) somewhat further advanced, with rudimentary embryo, *g*, at its base.

these leaves, which usually degenerate into scales, that the 'cone' so characteristic of this group is composed. The 'ovule' of the Gymnospermeæ corresponds in every essential particular with the 'large spore' of the Lycopodiaceæ; for, at the time when the pollen is shed, there is in it no germ-cell ripe for impregnation; but germ-cells are subsequently evolved in its interior, from a preliminary growth which is homologous to the 'prothallium' of the higher Cryptogamia, and within organs corresponding to their 'archegonia.' The interior of the ovule is at first filled with a mass of cells forming the 'nucleus' (Fig. 217, A, *a*), in the midst of which there is seen a peculiar cell (*b*), which is termed the 'embryo-sac.' This enlarges, and becomes filled with cells by free cell formation; thus forming an 'endosperm,' which occupies a considerable part of the interior of the ovule (B, *b*). At this time, the pollen-tubes usually begin to insinuate themselves into the tissue forming the apex of the nucleus, having passed through the open canal (micropyle) at the summit of the ovule (B, *c*). Certain of the cells at this end of the endosperm (prothallium) then enlarge, and develope themselves into the bodies that have been termed 'corpuscles;' the number of which, in each ovule is usually from three to five (C, *d*). The summit of each corpuscle (seen in section at D, *e*) is a quadrifid papilla, formed of four cells surrounding an intercellular passage, just as in the archegonium of Selaginella (Fig. 214, E); its interior is occupied by loosely arranged free-cells (D, *d*), but at the bottom of its cavity is observed a large and peculiar cell, the 'embryonal vesicle.' The pollen-tube at last finds its way down to the summit of the 'corpuscle' (E, *c*); and soon afterwards the embryonal vesicle (*f*) becomes greatly enlarged, and a free cell is formed in its interior (F). This cell first divides by a vertical septum into two collateral cells (G); and these again, by another vertical septum at right angles to the first, into four; and these are again divided by a cross-partition, so as to form a pro-embryo composed of eight cells (H). The four lower cells, which become detached one from another, develope themselves by duplicative subdivision into as many rudimentary embryoes; whilst the four upper, multiplying longitudinally, and becoming greatly lengthened, form the 'suspensors,' whose growth carries downwards the rudimentary embryoes at its lower end, into the substance of the nucleus (I—M). Of these four embryoes, three are subsequently arrested in their development; so that only one is found in the mature seed. This process occupies an unusually long period; the seed not being ripened, in many Coniferæ, in less than two years.—The apparent complexity of this process in Gymnospermeæ, as compared with the simpler type of its performance in the Angiospermous Phanerogamia, will be found to consist merely in the preliminary development of the 'endosperm,' with its 'corpuscles,' within the embryo-sac; this being interposed (as it were), like the development of the prothallium and archegonia in the higher Cryptogamia, previously to the evolution of the 'embryonal vesicle,' which is elsewhere a primary formation within the embryo-sac.

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* Op. cit., p. 126, *et seq.*

502. The mode in which the Generative function is performed in *Phanerogamia* generally, has been the subject of a vast amount of discussion within the last few years; but in regard to its main points there is now so close an agreement among a large number of careful and conscientious observers, that the continued dissent of a few can scarcely be admitted as invalidating the accuracy of their conclusions.*—The general

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* The most important question on which there is a discordance of opinion, is that of the origin of the embryo; for whilst the doctrine first advanced by Amici, that it is evolved

structure and arrangement of the sexual organs having been already described (§ 30), we have now only to consider the details of the operations of which they are the instruments.

503. The germ-cells, now distinguished as *pollen-grains*, are developed within the parenchyma of the leaf-like organ that is subsequently to become the 'anther,' by a curious process, which seems to indicate the necessity for a special elaboration or preparation of their contents. According to Mr. Henfrey,* the first stage is the development of new cells within those of the ordinary parenchyma; the wall of each of these new cells enclosing the entire contents of that within which it is formed, and the young cell thus entirely filling the original cavity. When the young cell is completely formed, the wall of the cell that enclosed it decays-away, leaving the young cell free; and this is now known as one of the 'parent-cells' of the pollen. The protoplasma of each of these parent-cells then divides into two, and then into four portions; so that two septa, generally crossing at right angles, are found, dividing the original cavity into four cells, each of which generally has the form of a quarter of a sphere. Within every one of these cells, termed by Mr. Henfrey the 'special parent-cell,' a new cell-wall is developed around its contents; and this new cell, the 'pollen-grain,' is afterwards left free by the dissolution of the walls of the 'parent-cells' and of the 'special-parent-cells,' within which it was enclosed.—The pollen-grain, like other cells (§ 347), possesses two envelopes, of which the inner one is extremely delicate, whilst the outer is firm and resisting, in virtue of the peculiar deposit which takes place upon it while yet within the pollen-cell. This deposit frequently forms prominent ridges, which may cross

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from an 'embryonic vesicle' contained within the embryo-sac, has been confirmed by the observations of Mohl, Karl Müller, Hofmeister, Tulasne, and Henfrey, the assertion of Schleiden, that it is developed within the extremity of the pollen-tube has received the support of his pupil Schacht, and of some others of less note. Although the Author has not himself made this question the subject of personal investigation, yet looking on the one hand to the very high character of the observers who have confirmed Amici's statements, and considering, on the other, the large number of instances in which the statements of Prof. Schleiden have had to be set aside, he can entertain no hesitation as to the truth on this point. The following are the principal memoirs which those who desire more detailed information on this subject should consult:—Prof. Amici 'On the Fertilization of *Orchidaceæ*,' translated in "Ann. des Sci. Nat.," 3e Sér., Botan., Tom. VII., p. 193; Von Mohl 'Ueber Entwickelung des Embryo von *Orchis Morio*,' in "Botan. Zeitung," July 2, 1847, translated in "Ann. des Sci. Nat.," 3e Sér., Botan., Tom. IX., p. 24; Karl Müller, 'Beitrage zur Entwickelungs-geschichte des Pflanzen-embryo,' in "Botan. Zeitung," Oct. 15, 22, 29, 1847, translated in "Ann. des Sci. Nat.," 3e Sér., Botan., Tom. IX., p. 33; Hofmeister 'Untersuchungen des Vorgangs bei der Befructung der *Œnotheren*,' in "Botan. Zeitung," Nov. 5, 1847, translated in "Ann. des Sci. Nat.," 3e Ser., Botan., Tom. IX., p. 65; also 'On the Development of *Zostera*,' in "Botanische Zeitung," Feb. 13, 20, 1852, translated in "Taylor's Scientific Memoirs," Nat. Hist., 1853, p. 239; Tulasne 'Etudes d'Embryogénie Végétale,' in "Ann. des Sci. Nat.," 3e Sér., Botan., Tom. XII., p. 23; and Henfrey 'On the Reproduction of the Higher Cryptogamia and the Phanerogamia,' in "Ann. of Nat. Hist.," 2nd Ser., Vol. 1852, p. 448;—on the other side, Schleiden, "Principles of Scientific Botany" (translated by Dr. Lankester), pp. 402, *et seq.*; and Schacht, "Entwickelungs-geschichte des Pflanzen-Embryon" (Amsterdam, 1850), abridged in "Ann. des Sci. Nat.," 3e Sér., Botan., Tom. XV., p. 80.

* "Reports of British Association" for 1848; Part II., p. 84.—This account corresponds with that of Naegeli in nearly every essential particular, save that the latter regards the new cells as originating in separate nuclei or cytoblasts, which Mr. Henfrey affirms not to be the case.

each other, so as to leave reticulations of a very regular and beautiful aspect; and it always seems to be thinner than usual in one or more spots. The contents of the pollen-grain have at first the character of the ordinary protoplasma; but gradually the fluid becomes more watery, and the granular particles more distinct. Of these particles, some appear to be mucilaginous, others to be oily, and others, again, to consist of starch. In an early stage of the development of the pollen-cell, a regular 'cyclosis' may be seen within it; but this ceases some time before its maturation, and a mere molecular movement is then all that remains.

504. The *ovule* is developed in the midst of the parenchyma of the *placenta* (which is the part of the carpellary leaf to which the ovules are found attached), and commences as a single cell, which, by successive subdivisions forms a projecting mass, that sometimes remains 'sessile' upon the placenta, and sometimes becomes partially detached from it, remaining connected only by a 'peduncle.' The mass of cells that is first formed, is that which afterwards constitutes the *nucleus* of the ovule; as its development proceeds, it becomes enveloped in one, two, or even three coats, which are formed by the multiplication of cells that at first constitute merely an annular enlargement at its base. The apex of the nucleus, however, is never entirely covered-in by these investments; a small aperture being always left through them, which is called the *micropyle.* In the interior of the nucleus is a large cavity, which appears to be formed by the enlargement of one of its cells, that grows at the expense of the surrounding tissue (Fig. 218, A). This cavity, which is termed the *embryo-sac,* is at first filled only with protoplasma; but some little time *before* fecundation, there are seen in it a certain number of free cell-nuclei, rarely fewer than three, and frequently more; these are observed especially near the apex or micropylar end of the embryo-sac (C), although, when they are very numerous, some of them are seen near its base. Around these nuclei, free cells of a spheroidal form are developed (D), of which only one is usually destined to be fertilized, and to be the original of the future embryo; all the rest subsequently disappearing, as if their function were to elaborate or prepare the nutriment for the developing germ.—The maturation of the pollen-grains takes place contemporaneously with that of the ovules; and when the former are set-free by the rupture of the anther, they fall upon the stigma, and begin to absorb the viscid secretion which bedews its surface.* In consequence of this absorption, the inner membrane or proper cell-wall becomes distended, and either breaks through the thinner points of the external envelope, or pushes this before it, so as to form one or more long slender projections, which are known as the *pollen-tubes.* These

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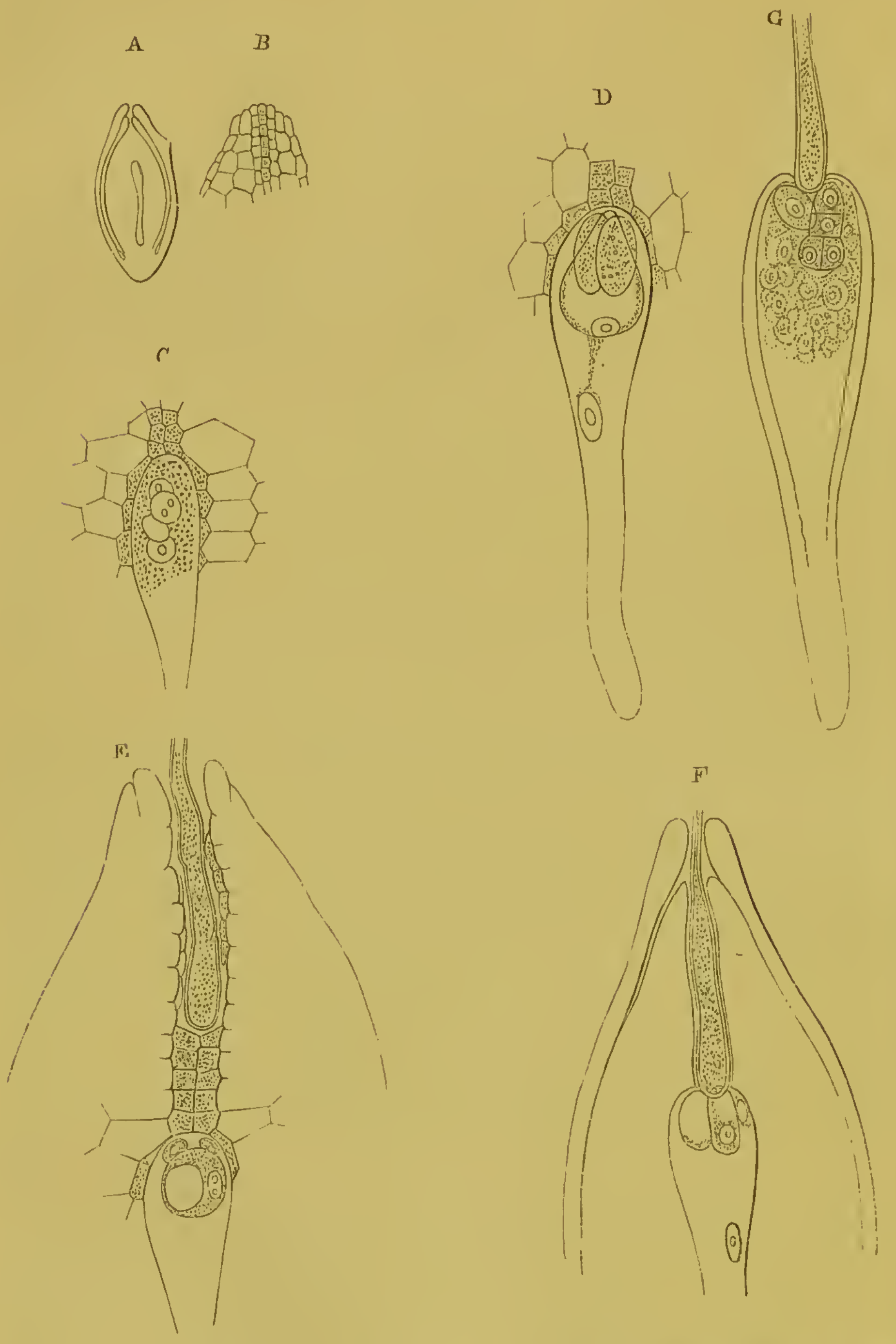
* In diœcious Phanerogamia, the transmission of the pollen from the staminiferous to the pistilliferous individuals is sometimes accomplished by the wind, and sometimes (as in the Fig) by the agency of Insects. A very curious modification of the ordinary plan is presented in the *Vallisneria spiralis;* for whilst its pistilline flowers are borne on long spiral foot-stalks, which enable them to adapt themselves to varying depths of the water which they inhabit, so as always to float on its surface, its staminiferous flowers detach themselves before they are quite mature, rise freely to the surface, and open themselves amidst the pistilline flowers, which are fertilized by the pollen they discharge. This phenomenon is of peculiar interest, from its relation to analogous phenomena in the Animal Kingdom (§ 546).

insinuate themselves between the loosely-aggregated cells of the style, and grow downwards until they reach its base; a distance, in some

FIG. 218.



Development of the Embryo of *Œnotheraceæ*:—A, longitudinal section of non-fecundated ovule, showing the embryo-sac in the midst of granular mucilage;—B, longitudinal section of the mammillary projection of the nucleus;—C, upper portion of the embryo-sac, with the surrounding cellular tissue, from a more advanced embryo;—D, the same at a later period;—E, advance of the pollen-tube towards the nucleus;—F, contact of the pollen-tube with the summit of the embryo-sac, the embryonal vesicle in close proximity;—G, embryo beginning to form within the embryonal vesicle after fecundation.

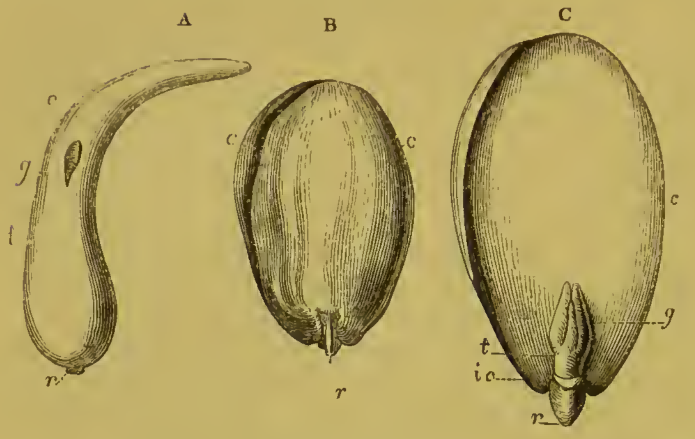
cases, of several inches. Arrived at the ovarium, they direct themselves towards the micropyles of the ovules; and entering these, they make their way towards the embryo-sac, usually through a channel formed by the diffluence of a sort of cord of peculiar cells, that previously passed from the apex of the embryo-sac to that of the mammillary protuberance of the nucleus (B, E). The extremity of the pollen-tube then impinges upon the apex of the embryo-sac itself (F), and sometimes pushes it slightly inwards, so as to have given origin to the idea that it enters its cavity. There is not, however, any direct communication between the cavity of the pollen-tube and that of the embryo-sac; but whatever admixture may take place between their contents, must occur by transudation through their respective limitary membranes.

505. It is in such an admixture, that the act of Fertilization appears essentially to consist; for soon after the contact of the pollen-tube with the embryo-sac has taken place, it becomes apparent that *one* of the cells which the latter contained is now undergoing rapid enlargement, and that the remainder are in a state of degeneration. This cell, whose previous existence appears to be now indubitably ascertained, and which is the real 'germ-cell,' is distinguished as the *embryonal-vesicle;* and it is within this, when fertilized, that the embryonic structure originates. The early processes of development correspond precisely with those which have been already described as taking-place throughout the whole of the inferior tribes; for the primordial cell formed within the embryonal vesicle as the result of its fecundation, gives origin by transverse fission to a pair; this, again, to four (G); and so on, it being usually in the *terminal* cell of the filament so generated, that the process of multiplication chiefly takes place, just as in the Confervæ. At the same time, the mucilaginous matter which fills up the embryo-sac becomes organised and converted into loose cellular tissue, which constitutes the 'endosperm;' the cells being formed around free nuclei (§ 351). As in most other cases, however, in which this mode of cell-formation occurs, the tissue thus produced is very transitory in its character; for it usually deliquesces again, as the embryonic mass increases in bulk and presses upon it; and thus the only purpose which it can be imagined to serve, is that of elaborating the nutriment for the growing fabric, which may well be supposed to need such a preparation, in virtue of its superior importance and permanence.

506. The Embryo, which is at first a simple filament, usually enlarges most at its lower extremity, where its cells are often multiplied into a somewhat globular mass; of this mass, however, by far the larger proportion is destined to be evolved into the *cotyledons* or seed-leaves, whose function is limited to the earliest part of the life of the young plant; the rudiment of the *plumula*, which is to be developed into the stem and leaves, being at first scarcely visible. The more prolonged portion, which points towards the micropyle, is the *radicle* or rudiment of the root. These parts increase in some Dicotyledons, until they have absorbed unto themselves all the nutriment contained, not only in the embryo-sac, but also in the tissue of the nucleus itself; so that the seed, at its maturity, contains nothing but the embryo, of which the cotyledons are rendered thick and fleshy by the amount of nutritious matter which they have absorbed. This is the case, for example, in the Leguminous family generally, and a good illustration of it is furnished by the Almond (Fig. 219,

B, C); in such instances, the remains of the nucleus and of the embryo-sac coalesce to form an envelope to the embryo within the proper seed-coats. But in many other plants, the cotyledons remain foliaceous; so that, at the maturation of the seed, a large proportion of the nutriment which the ovule originally contained, is unabsorbed into the embryo, and remains on its exterior, constituting the *perisperm* or *albumen*. This is the case in the seeds of many Dicotyledons, as the Castor-oil and the Ash; but it is universally true of Monocotyledons. The form which the embryo presents in the latter, is quite different from that which it possesses in the former; for the single cotyledon is rolled round the plumula, so to speak, in such a manner as completely to enclose it, except where a little fissure is left by the non-adhesion of the edges of the cotyledon (Fig. 219, A, *g*), through which the plumula subsequently escapes. This arrangement is quite conformable to the relation which exists between the stem and all the subsequent leaves of Monocotyledons in general; for they, too, ensheath the axis at their base, as is well seen in the Grasses.

Fig. 219.



A, Monocotyledonous Embryo of *Potamogeton perfoliatum*; *r*, radicle; *t*, caulicle; *g*, plumula; *c*, cotyledon;—B, Dicotyledonous embryo of *Amygdalus communis* (Almond), showing *r* the radicle, and *c c* the cotyledons;—C, the same with one of the cotyledons removed, so as to expose the plumula *g*, and the caulicle *t*, at the base of which is seen the mark of attachment *i c* of the second cotyledon.

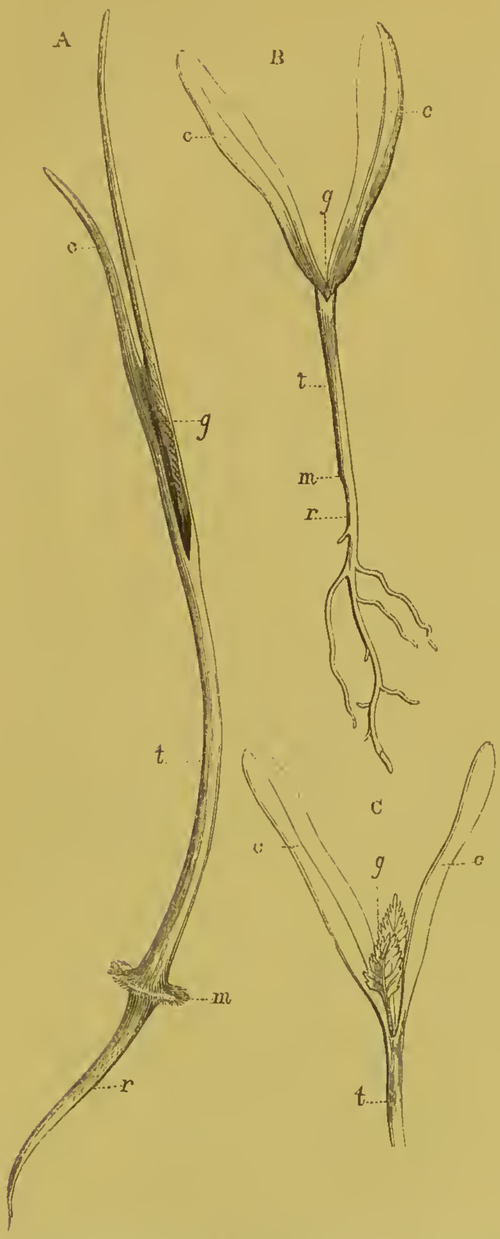
507. The Seed, when completely matured, becomes detached from the placenta, and is set free by the opening of the seed-vessel. In this condition it may remain for a great length of time, in a state of complete inaction, without the loss of its vitality, provided that it be secluded from influences which would either force it into growth, or tend to occasion its decomposition; and in fact, this period of 'dormant vitality' may be protracted, in the case of many seeds, to an extent to which there seems no limit. (See General Physiology.)—The conditions which are absolutely requisite for the *Germination* of seeds, are water, oxygen, and a certain amount of warmth; and the process is favoured by the absence of light. When the seed imbibes moisture, the embryonic tissue swells, and the radicle is advanced towards the micropyle, whilst at the same time the seed-coats are commonly ruptured by the internal distension. During these processes, certain chemical changes take place in the starchy matter contained in the perisperm or absorbed into the cotyledons, in virtue of which it is converted into a saccharine compound, probably to be blended with albuminous matter to form a protoplasma for the nutrition of the growing tissue; and these changes involve the production of a certain amount of carbonic acid, by the union of the carbon of the seed with atmospheric oxygen (§ 274). Hence it is that oxygen,

as well as water, is required as a condition of this process; and that light is rather injurious than beneficial, since it tends to *fix* the carbon in the vegetable tissues. This conversion is effected by the instrumentality of the *diastase* stored-up in the seed (§ 360). Whilst thus living upon organic compounds previously elaborated by an agency other than its own, thriving best in the dark, and imparting to the air a large quantity of carbonic acid, the germinating plant may be regarded as physiologically very much in the condition of a Fungus.—The radicle, however, becoming prolonged by the imbibition of water and by the formation of new tissue at its extremity, tends to grow downwards into the soil; and the plumula then begins to elongate itself in the opposite direction, whilst the minute protuberances which it previously bore, evolve themselves into leaves. The cotyledonary portion is usually the last to quit the seed-coats, and somtimes it remains and withers there; but usually it is carried upwards to the surface, acquires a green colour, and performs the functions of a leaf. In the germination of such Monocotyledons as thus send up their cotyledon (Fig. 220, A), this organ very closely resembles the subsequent leaves in form, and in its relations to the stem; in that of Dicotyledons, on the other hand, the plumula rises-up from between the cotyledons (B). In many Gymnosperms, the cotyledons are multiple, forming a sort of verticil, resembling that of their true leaves. —The germinating plant continues to appropriate the nutriment stored-up in the cotyledons or remaining in the perisperm, and to employ it as the material for the extension of its permanent fabric; and by the time that this store has been exhausted, the roots and leaves are sufficiently developed to enable them to perform their respective functions, and thus to minister to the further extension of the structure. It is then only, that true woody fibre and vessels begin to show themselves in the axis; for during the previous stages of embryonic development, its tissue has been cellular only; and an almost exclusively cellular organisation is common to young parts at all subsequent periods.

508. The plumula may be regarded as the first 'terminal bud' of the growing plant; and with its short stem and radicle, forms a *phyton.* A tree, to whatever dimensions it may attain, is but an aggregation of such phytons; and these are formed in continuous development from the one thus immediately evolved from the seed. The elongation of the stem is provided-for by the development of a succession of terminal leaf-buds; each, as the leaves have performed their functions and have died-off, being replaced by another. But in nearly all cases (Palms being the principal exceptions), lateral leaf-buds also are developed, which are, so to speak, the terminal leaf-buds of the branches that are to grow-forth from the axis (Fig. 32, A, *d*, *d*); and when these have been developed into branches, they in their turn put-forth other lateral buds; and thus an unlimited amount of ramification may take place around the central axis. In all cases, however, the buds originate in the medullary tissue of the stem or branches; being, in fact produced by the multiplication of its cells at certain points, which usually have some definite relation to each other, so as to give to the whole structure a more or less symmetrical character (§ 29). Thus we have a multitude of parts evolved, which are mere repetitions of each other, and which have scarcely any relation of mutual dependence; and these parts, when detached from the common stock, and placed under

circumstances favourable to their growth, will preserve their vitality, and will develope themselves into organisms in all respects similar to that from which they were removed. Such a detachment of leaf-buds sometimes takes place spontaneously,* and constitutes the ordinary mode in which the plant is propagated. In other instances, nothing more is necessary than the artificial separation of the leaf-buds; thus the Sugar-cane is ordinarily propagated by dividing the stem into as many pieces as it possesses lateral buds, and burying these in the ground; and, in like manner, the Potato is multiplied by the division of its 'tuber' (which is really an underground stem) into as many pieces as it has 'eyes.' So, again, there are many trees and plants, of which the branches will take root, when merely cut or broken off, and placed with their ends in the soil; and such, therefore, may be propagated by 'slips' or 'cuttings.' In many other cases, however, more care is necessary; the buds not possessing enough developmental capacity to ensure the production of roots after their complete detachment from the stock; and the evolution of such buds is provided-for, either by connecting them with a new stock to which they become adherent, so that it stands in the place of the stem and roots of that from which they have been removed, which operation is termed 'grafting;' or by delaying the final detachment until they have already struck root into the soil, as is practised in the operation of 'layering.'

Fig. 220.



A, Germination of Monocotyledonous embryo of *Zanichellia palustris*; *r*, radicle; *m*, collar; *t*, stem; *g*, plumula; *c*, cotyledon;—B, germination of Dicotyledonous embryo of *Acer negundo* (Maple); *r*, radicle; *m*, collar; *t*, stem; *g*, plumula; *c c*, cotyledons; —C, the upper part of the same in a more advanced state.

509. Now in all these cases, the plant, which is developed from the

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* The following list of plants that habitually propagate by spontaneously detaching bulbels (the first two reproducing themselves, so far as can be ascertained, in this manner alone), has been furnished by M. Decaisne;—*Lunularia vulgaris*, *Lemna gibba*, *Dentaria bulbifera*, *Dioscoræa*, *Globba amarantina*, *Gagea villosa*, *Ornithogalum umbellatum*, and *Lilium bulbiferum*.

detached *bud*, partakes of the characters of the stock from which it sprang, much more fully than does the plant raised from *seed;* for whilst the latter continues the *species* only, the former reproduces the particular *variety.*[*] Hence, when it is desired to multiply a certain kind of fruit-tree, the buds are employed, rather than the seeds. But this method of propagation cannot be carried to an indefinite extent; for although it may not be true (as stated by some), that the life of the 'graft' will only last as long as that of the 'stock' from which it was taken, yet it is almost invariably found that varieties of trees and plants which are thus multiplied, lose their vigour and 'die out' after a certain lapse of time. They all partake, in fact of the 'germinal capacity,' which was engendered by the original generative act; and every multiplication of parts by the continued subdivision of cells must be regarded (so to speak) as an expenditure of that capacity; so that there is necessarily a limit to this operation, although the limit seems to be much less strict when the extension takes place in structures of a low type, than when *development* of a higher kind is required in addition to mere *growth.*

510. Now from attaching too exclusive consideration to the fact of the independent vitality of leaf-buds, many Botanists have come to the conclusion, that a composite tree is to be regarded, not as one individual, but as *an aggregate of individuals;* and that each series of buds should rank as a *distinct generation.* But if such be the acceptation in which the terms 'individual' and 'generation' are to be employed, it will be found that they must be rendered still more comprehensive. In the first place, if we look to what a part may *become,* rather than to what it *is,* as our test of individuality, we must include under this designation, not merely the leaf-buds, but the leaves, of many plants (such as the *Bryophyllum*), which possess the power of developing buds and roots from their margins; and this view has been adopted by Prof. Owen, who regards every leaf, and even every modified form of the same fundamental type,—each sepal, petal, stamen, and carpel of a flower,—as entitled to rank as a distinct being.[†] But if we go *so* far, we must go further still, and admit that each *fragment* of a leaf is entitled to be characterised as a distinct individual; since the leaf of Bryophyllum, even when divided into numerous segments, will continue to vegetate under favourable circumstances, and will evolve itself into a complete plant; and the whole of such a leaf, therefore, must be regarded as an aggregate of individuals. Such a doctrine was actually propounded in regard to the *Hydra,* when its extraordinary power of developing the whole from any single part was first discovered (§ 473); but no Physiologist would at present support such an idea; and as its singleness is not now disputed on account of its repetition of similar parts, and its almost unlimited reproductive capacity, neither (as it seems to the author) should that of the Plant. For it would be just as legitimate to regard as 'distinct individuals' the several tentacula which form a circle round the mouth of the Hydra, as it is to assign this rank to the several petals of a corolla, or to the carpels of an ovary. The cells of the simplest

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[*] It would seem, however, as if, in the case of *annual* plants, the variety is more steadily transmitted by seed; such is certainly true of the Cerealia, in which we find repeated, not merely the general modifications induced by cultivation, but the more particular forms that occasionally arise *de novo.*

[†] See Prof. Owen's "Parthenogenesis," p. 54, *et seq.*

Protophyta *may* be allowed the designation of 'distinct individuals,' if by this be implied no more than that they are complete in themselves, and have the power of separate existence. But although thus functionally independent, they are organically related to each other in the same degree as are the component cells of the most heterogeneous fabric, whether Vegetable or Animal; for the aggregate mass of cells of a Palmella or a Desmidium, produced by the subdivision of one 'primordial-cell,' is clearly the homologue of the entire embryo of the Phanerogamous plant, which is (like it) composed of a mass of cells, evolved by successive subdivision from the fertilized embryonal vesicle; and if every new pair that is produced by the subdivision of a pre-existent cell, is to be regarded as a 'new generation' in the one case, it must in the other also.—The confusion which at present prevails in regard to this subject, and which has given rise to the strangest misapprehensions, has arisen from that very confusion of *functional* and *homological* relationship, which formerly obstructed the progress of Philosophical Anatomy (see CHAP. I.); and will not be dissipated, until a clear distinction shall have been drawn between the two. The question of 'individuality,' in the *usual* acceptation of the term, is one entirely of the former kind; for its limits are not established by any other rule than functional capacity; and nothing can be more variable than its degree. Thus, such an individuality exists in the segments of the leaves of one plant, in the entire leaves of a second, in the leaf-buds of a third, in the branches of a fourth, and in the entire axis and appendages of a fifth; whilst in a sixth, the individuality shall entirely depend upon circumstances, its buds not being able to sustain their vitality after their detachment, unless their development be favoured by engrafting them on a living stock.* But in its *scientific* aspect, like the question of 'generations,' it is one entirely of the latter nature, and can only be determined by adhering strictly to homological principles.

511. Another view has been suggested, which at first sight appears more worthy of adoption; namely, that a *tree* may be regarded as a collection of *annual plants;* the buds of each year giving origin to those of the next, when their own term of existence is expired.† In a Potato, for example, it is argued that each year's growth terminates in the production of tubers or underground stems, which contain the buds that are to be developed into distinct and independent plants in the ensuing season; these in their turn giving origin to tubers, whose buds are to be developed in a subsequent year. Now what is true of the potato, it is urged, is true of an ordinary tree; the only difference being, that the remains of previous growths are persistent, although dead, and that thus a permanent stem is formed, on which every generation of buds is developed, as it were parasitically, and to which each generation makes an addition that is left behind when the leaves decay.—In this, as in the preceding doctrine, however, it appears to the author that too much account is made of the

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* If the individuality of *leaf-buds* be maintained, because they will continue to exist as grafts, the same attribute ought to be allowed to parts of *animals*, e. g. teeth, testes, ovaries, &c., which have been removed from one animal and implanted in another, and which have formed new attachments to the latter, and continued to grow.

† See Dr. Harvey 'On the Nature, Longevity, and Size of Trees,' in the "Edinb. Philos. Journ.," Jan. 1847.

leaves, and too little of the other parts. The leaf is by no means, as some have represented it, the entire plant; it is only the most important of the vegetative organs of the plant. But it cannot maintain an independent existence (save in a few rare cases in which the leaf possesses unusual absorbent powers), unless it is able to develope roots; and it cannot perform the generative act, unless it can evolve the flower. Now other parts of the plant may possess the same independent vitality, if only, like leaf-buds, they can evolve the organs in which they are themselves deficient; thus there are many trees which can be propagated by cuttings of their roots, these having the power, under favourable circumstances, of putting-forth leaves; and there are others which can be multiplied in like manner by division of their stems, each cutting being able to put-forth both leaves and roots.

512. Further, whilst too much account is thus made of the leaves as integral components of the plant, too little is made of the *general cellular basis*, from which the leaves originate, and which retains its vitality in every stem, through the whole period of its existence. This cellular basis is the continuous product of that in which the whole fabric has its origin; it is that of which the leaves are offsets, developed for a particular purpose (the elaboration of nutriment for the axis and its other appendages), and ceasing to exist when that purpose is answered; and it retains the power of giving origin to buds from *any part of it* that may be stimulated to increased development. For although it may be quite true that, under *ordinary* circumstances, each year's growth of buds originates in the new tissue formed in the preceding year, yet this tissue is but the extension of the general cellular basis; and, under *extraordinary* circumstances, portions of this at a great distance from the last-formed buds, may develope a new set of foliaceous organs.*—Moreover, the doctrine in question is entirely inapplicable to the case of the *leafless* Phanerogamia, such as the *Cactaceæ*. The succulent mass of which their stems are composed, is obviously homologous with that general cellular basis, of which the axes of all the higher plants consist at an early stage of their development, and from which the leaves are developed wherever they exist; whilst its foliaceous surface performs the functions of the leaf, the two organs not being here separated, nor their functions specialised. Now it cannot but be admitted, that it is this cellular mass, which in the Cactaceæ constitutes *the plant;* since here no separate leaves are evolved. And further, we must regard the whole as one integer, unless we are prepared to say that every separate portion of this mass, which can maintain an independent existence, is to be regarded as endowed with a distinct

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* The following, for example, occurred within the Author's own observation. An Elm-tree, which grew to the height of nearly thirty feet before it gave forth any branches, had its upper part entirely broken-off in a gale of wind, and the stem was left standing, entirely bare of foliage. Its death was considered almost inevitable (and such it was upon Dr. Harvey's theory); but it was thought desirable to give to it a chance of recovery, and nothing else was done than to slope-off the top of the stump, so as to prevent the lodgment of rain. The next spring, a great number of buds were developed, along nearly the whole length of the stump, where no buds or branches had grown for many previous years; these, in process of time, became branches; and the topmost branches having gradually changed their direction (in accordance with the well-known law) from the horizontal to the perpendicular, now appear like continuations of the stem, and the tree, after an interval of about 27 years, has quite recovered its symmetrical appearance, although its aspect is of course very different from that which it presented before the accident.

individuality.* The duration of this cellular stem of the Cactaceæ is extremely prolonged, its life being very slow; so that there are undoubted instances of plants of this order continuing to exist for 100 years; and their probable term of life is very much longer. There need not, therefore, be the least difficulty in admitting the continued vitality of the general cellular basis of the stem of an ordinary tree, notwithstanding that it may have attained the age of some hundreds or even thousands of years. The parts first formed may have long since decayed away, but a new growth is continually taking place; for the 'cambium-layer' (in the Exogenous stem) is in a state of continual increment, and the proximity of leaves is not required for the growth of the additional layers of wood and bark into which it developes itself, nothing else being needed than a supply of elaborated sap, which may have been prepared by the leaves of remote parts of the fabric (§ 353).

513. There appears, then, to be no medium between, on the one hand, regarding the entire fabric developed from a single generative act (i. e. the fertilization of a single 'germ-cell' by the contents of a 'sperm-cell') as forming *one organism*, however great may be the multiplication of similar parts, or however independent these parts may be of each other; and the including every product of its own development, whether contemporaneous or successive, as *one generation*;—or, on the other hand, attributing a distinct individuality to every component of the most complex organism, and designating every augmentation of the number of its cells, by the subdivision of those previously existing, as the production of a new generation. In either case, it must be freely admitted, we are forced to do a certain violence to our ordinary conceptions; but if, on the one hand, it seems strange not to admit the proper individuality of a completely independent being (such as a potato-plant which has been developed, in common with several others, from a single tuber), nor to allow that in developing itself from a bud into a complete plant, and in putting forth its leaves and flowers, and in maturing its seed, it passes through a complete generation; on the other hand it seems yet more absurd to regard the human organism, or any other composite fabric, as made up of a congeries of individuals, and to regard each of these as entering upon a new generation whenever its component cells may have been renewed. And it may be the wisest course, perhaps, to invent new terms, rather than to distort the meaning of those in common use.

514. If, now, we take a retrospect of the whole series of phenomena of Vegetable Reproduction, we see that in all the cases (by far the larger proportion) in which a true Generative act is known or believed to take place, the fertilized cell, which is the immediate product of this act, gives origin, by successive subdivisions, to an immense congeries of cells, each having a certain degree of independent vitality;—that in the simplest Protophytes, each one of these detaches itself from the rest, and lives for and by itself, in a state of *functional* independence of them, except so far as it requires another to conjugate-with, whilst there is yet the same *homological* relationship among them all, as exists among the component cells of any single plant developed from seed;—that at a little higher

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* It has been shown that small fragments of the Cactaceæ may thus be made to grow, by grafting them upon other plants of the family, even though the generic alliance be not very close. See note in p. 524.

elevation in the scale, the cells developed from one primitive germ remain attached to each other, and form masses of almost unlimited extent (such as the gigantic fronds of marine Algæ), all whose parts are in like manner homologically related, whilst they nevertheless continue so similar in their endowments as to possess a great degree of functional independence;—that as we ascend yet higher, we find the evolution of the primary embryonic cell no longer consisting in the multiplication of homogeneous parts, but involving the development of some of the products of its subdivision into forms very dissimilar to its own and to each other; and of the organs so developed, a certain combination is requisite for the maintenance of vegetative activity;—but that even where a considerable degree of mutual dependence is thus established, as in the most heterogeneous and highly-specialized Vegetable organism, there is usually such a multiplication of similar parts, that many of these can be removed without serious injury to the remainder; whilst there is frequently also such an amount of reproductive capacity still remaining in each principal organ, that, even when separated from the rest, it can develope whatever parts are deficient, and can thus maintain its existence independently of them. It is only when the whole series of phenomena is thus comprehensively surveyed, that we rightly appreciate the real relationship of the component organs of the most perfect Phanerogamous plant, or of the isolated cells of the simplest Protophyte.

515. The true relations between the Generative operations of the different groups we have been surveying, are considerably obscured by the entire want of conformity which exists among them, as to their relations with the Vegetative or developmental phases of Plant-life. Thus, if we start from the 'primordial cell' of the embryo, we find this evolving itself by duplicative subdivision into that leafy stem which is accounted 'the plant' in Phanerogamia; and the same happens in the Ferns and their allies. This 'vegetative system' in the Angiospermous Phanerogamia gives origin by continuous gemmation to the 'generative system,' which consists of the flowers bearing ovules and pollen-grains; and no *obvious* phase of existence intervenes between the development of the embryo-sac contained in the ovule, and the origination of the primordial cell of the embryo as the consequence of fecundation. In the Fern, on the other hand, the 'vegetative system' does not at once develope the 'generative system,' but produces a number of detached 'spores,' each of which developes itself independently into a 'prothallium' bearing the essential generative organs; yet this prothallium is shown, by tracing its homologue in the Lycopodiaceæ and Gymnospermeæ, to be but a higher development of the fugitive endosperm-cells of the ovule in the ordinary Phanerogamia, which thus constitute the sole representative of the prothallium in Cryptogamia. But when we go to the Mosses and Liverworts, we find the immediate product of the generative operation to be a mere sporangium instead of a complete plant; and that which in these tribes constitutes 'the plant' is evolved from the spore, being a still higher development of the prothallial condition. And descending to the *Characeæ*, which may be considered as affording a typical example of the phase of Plant-life presented by the lower Cryptogamia, we not only find the prothallium, with its antheridia and archegonia, ranking as 'the plant,' but, as each primordial cell developes itself, not into a sporangium

but into a new prothallium, we entirely lose sight of that phase which in the Mosses is represented by the development of the stalked spore-bearing capsule, in the Ferns by the development of the stem and spore-bearing leaves, and in the Phanerogamia by the evolution of the whole apparatus of leaves and flowers.*

3. *Reproduction in Animals.*

516. The condition of the Reproductive function in the lower part of the Animal kingdom, may be considered as almost precisely analogous to that which it presents among the higher Plants; for, on the one hand, we find the act of *Generation* performed under circumstances, which on the whole most resemble those under which it takes place in the Phanerogamia; whilst, on the other, we see that this is by no means the only—frequently not even the chief—mode in which the multiplication of the original stock is provided-for, repetitions of that stock being produced by a process of self-division or of gemmation, so that a large number of the independent beings ordinarily designated as 'individuals' may result from one act of generation. Such beings, as already shown in regard to Plants, have a very different relationship to one another, from that which is possessed by the perfect individuals among the higher classes of animals, every one of which contains in itself the entire product of the act of generation in which it originated; being, in fact, as nearly related to each other *by descent*, as are the several parts of the body of the latter, although possessing a functional independence that enables them to maintain a separate existence. As it is peculiarly important that the true nature of this relationship should be kept in view, *the detached portions of the stock originating in a single generative act* will be termed *Zöoids;* whilst by the words 'animal' or 'entire animal' (the equivalent of *Zöon*), will be implied, in the lower tribes as in the higher, the *collective product of a single generative act.*† Thus, the whole Zoophytic structure produced by continuous gemmation from a single ovum, will be considered as one animal; just as the whole product of a single seed is one plant. And as the *homological* relation of the parts to each other is not disturbed by their detachment, although they are rendered *functionally* independent, the detached gemmæ or zöoids of the *Hydra* (§ 534) are the real equivalents of the connected polypes of the *Laomedea* or other composite Hydroid Zoophyte (Fig. 99).

517. Further, as the multiplication of separate zöoids to any extent, is a process of exactly the same order as the growth of the composite structure in which they remain continuous with each other; and as this, again, is obviously of the same nature with the development and growth of the component parts of more heterogeneous organisms higher in the scale; it is clearly correct to include, under the title of *one generation,* in the former case, as in the latter, all that intervenes between one Genera-

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* For a fuller discussion of the homologies between Phanerogamia and Cryptogamia, see Mr. Henfrey 'On the Reproduction of the Higher Cryptogamia and the Phanerogamia,' in "Ann. of Nat. Hist.," 2nd Ser., Vol. IX., p. 441.

† The term *zöoid* was suggested to the Author by his friend Mr. Huxley; whose researches on the Acalephæ, carried-on in the Indian Seas, had led him independently to adopt precisely the same view of the relation of the two processes, as that for which he himself contends. By some of the French Naturalists, the word *Zöonite* has been used in nearly the same sense.

tive act and the next. If the phenomena be viewed under this aspect, it will be obvious that the so-called 'alternation of generations' has no real existence; since in every case, the whole series of forms which is evolved by continuous development from one generative act, repeats itself precisely in the products of the next generative act. The alternation which is very frequently presented in the forms of the lower Animals, is between the products of the *generative act* and the products of *gemmation;* and the most important difference between them usually consists in this,—that the former do not contain the generative apparatus, which is evolved in the latter alone. Not unfrequently, indeed, it happens that the detached zöoids are little else than combinations of generative organs with a locomotive apparatus adapted for their dispersion; or they may be, in the first instance, nothing else than buds, which will gradually evolve themselves into such a self-moving generative apparatus. Now the relation of these generative zöoids to those which are merely repetitions of the nutritive organs,—as, for example, the relation between the Medusa-buds and the Polypes of the Hydroid Zoophytes (Figs. 231, 232), —will be seen to be precisely the same as that of the flower-buds to the leaves of a Phanerogamic plant; and whilst we have in the *Vallisneria spiralis* (§ 504 *note*) an example of the spontaneous detachment of a bud in which one portion of the reproductive apparatus is already evolved, we have in the separation and diffusion of the spores of the Fern, a still more remarkable example of the detachment of gemmæ in the simplest possible condition, whose whole power of development is directed to the production of a true generative apparatus (§ 494). The generative zöoid may be merely a segment cast-off from the body at large, possessing no locomotive power, as in the case of the *Tænia* (§ 570); or it may contain a combination of generative and locomotive organs, as in the self-dividing *Annelida* (§ 576). It *may* possess, however, not merely locomotive organs, but a complete nutritive apparatus of its own, which is the case in all those instances in which the zöoid is cast-off in an early stage of its development, and has to attain an increased size, and frequently also to evolve the generative organs, subsequently to its detachment; of this we have examples in the *Medusæ* budded-off from Hydroid Zoophytes (§ 539), and in the aggregate *Salpæ* (§§ 557—560), as well as in other beings of similar completeness.

518. It has been already pointed-out, that what have been called the *fissiparous* and the *gemmiparous* modes of reproduction, are one and the same in their essential nature. Of the former we have the type in the multiplication of cells by *self-division,* which is best seen in the Algæ (§ 349); whilst of the latter we have the type in the multiplication of cells by *out-growth,* which is common in the Fungi (§ 350). The fissiparous method is the one most frequently witnessed among the Protozoa, whose condition most nearly approximates that of the Algæ; and it is occasionally seen, also, among Zoophytes. But in the latter class, as in all the higher tribes in which detached zöoids are produced, gemmation is by far the most usual method of their evolution.

519. The act of Generation is accomplished among Animals, as in the higher Plants, by the union of the contents of a 'sperm-cell' with those of a 'germ-cell;' the latter being that from within which the embryo is evolved, whilst the former supplies some material or influence necessary

to its evolution. These 'sperm-cells' and 'germ-cells' are usually developed in special organs, as in all the higher Plants; but in Sponges, as well, perhaps, as in some others of the lower Animals, they are evolved out of the midst of the ordinary parenchyma, and have no special locality. In many of the lower tribes, again, both sets of generative organs are developed in the same organism, and are capable of conjoint action; the animal is then said to be *hermaphrodite.* There are others in which both sets of organs exist, but they are not capable of conjoint action, so that the concurrence of two individuals is required, each fertilizing the other; such are also termed hermaphrodite, although they differ from the true hermaphrodites in not being self-fertilizing. In the highest members of the Radiated, Articulated, and Molluscous divisions, however, and in all Vertebrata, only one set of sexual organs is possessed by each individual, which is then designated as *monosexual.*—It has been a matter frequently and earnestly discussed, whether the embryo is to be considered as the product of the male or of the female portion of the generative apparatus; some having regarded the function of the sperm-cell as limited to the stimulation of the developmental process in an embryonic structure already evolved in the germ-cell; whilst others have considered that the real germ is produced in the sperm-cell, and that it is implanted in the germ-cell in the act of fertilization, to be henceforth dependent upon the female organism for the materials of its development. Now if we cast our eyes back upon the simplest Cryptogamia, we see that there is no proper distinction of male and female amongst them; but that each of the conjugating cells contributes an equal share to the result (§ 481). And the departures from this equality which are seen in the higher Plants, appear to have reference rather to the part to be taken by the female portion of the apparatus in aiding the subsequent development of the germ, than to its first production; and it seems probable that in the highest animal, as in the lowest plant, the formation of the primary cell of the embryo depends upon the actual intermixture of the contents of two cells, so that neither male nor female can be properly said to supply the germ by itself. Looking, however, to the very equal mode in which the characters of the two parents are mingled in *hybrid* offspring, and to the certainty that the *material* conditions which determine the development of the germ are almost exclusively supplied by the female, it would seem probable that the *dynamical* conditions are in great part furnished by the male.

520. The 'Sperm-cells' of Animals usually present a remarkable correspondence with those of the higher Cryptogamia, in the nature of their products; which, in the majority of instances, are self-moving filaments, or *Spermatozoa,* closely resembling the 'antherozoids' of Ferns, &c. These were formerly considered in the light of distinct and independent beings, and were termed 'spermatic animalcules;' but it is now universally admitted that they cannot be regarded as having any more independent vitality than blood-corpuscles or epithelium-cells, the latter of which, when ciliated, have at least an equal power of spontaneous movement. The forms of these spermatozoa present a certain degree of variation in the different groups of animals; but these variations cannot be said to have any correspondence with the zoological relations of the animals in which they are seen. Generally speaking, however, each spermatozoon

is composed of an ovoid 'body,' with a long filiform 'tail,' strongly resembling the antherozoid of the Fern (Fig. 210, D); and it seems to be by the undulations of this tail, rather than by cilia attached to the body, that the movements of the corpuscle are effected. An interior organisation was formerly described as traceable in the spermatozoa; but it is now certain that they are homogeneous, or nearly so, throughout; and that the supposed presence of a mouth, anus, &c., has no real foundation. These movements, however, are by no means of the same nature in all instances. Sometimes they consist of lateral undulations, as uniform and moderate in their rate as the vibrations of a pendulum; in other instances, a series of interrupted jerks is exhibited, the tail being coiled-up into a circle, and then suddenly uncoiled; other spermatozoa, again, advance with a regular screw-like or boring movement, turning rapidly on their axes; lastly, there are certain spermatozoa which have no motor power whatever, but the conditions of these, as will presently be shown, are altogether peculiar. It is obvious that the purpose of these movements is to bring the spermatozoa into contact with the germ-cell; and we shall see that the circumstances under which that contact takes place, vary greatly in different animals. For in some cases, the fluid containing the spermatozoa is conveyed into the interior of the female generative organs, so that it is ready to fertilize the germ-cells as soon as they are matured; in other instances, it is effused upon the ova at the time of their deposition; and in other cases, again, it is poured-forth into the surrounding liquid, and diffuses its fertilizing power far and wide through this, so as to act upon any ova which may have been deposited in its neighbourhood.

521. The vitality of the Spermatozoa is not usually long preserved, after they have been set free from the organism which produced them; but, like that of muscles, cilia, &c., it is manifested for a longer time in the case of cold-blooded animals, than in that of warm. Thus, the spermatozoa of Birds frequently cease to move within fifteen or twenty minutes after the death of the animal which produced them, or after their removal from its body; in the Mammalia, their motion continues for some time longer, especially if they remain enclosed in their natural organs; but the spermatozoa of Fishes will continue moving for several days after their expulsion. The most remarkable prolongation of their vitality is seen, however, when, after their expulsion from the male, they are received into the female generative organs; such is the case with many Mollusca and Articulata, which have a special receptacle or *spermotheca* for storing-up the seminal fluid, in order that it may fertilize the ova as they are successively developed; the spermatozoa remaining active within this, even for some months. Indeed it appears from the researches of Mr. H. Goodsir,* that in certain Crustacea the conclusion of the development of the spermatozoa themselves ordinarily takes place in this situation; their formation not being nearly complete, at the time when they leave the organs which evolved them. Even in Mammalia, their movements have been found to continue unimpaired for some days after their introduction within the female organs.† The movements of the

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* 'The Testis and its Secretion in the Decapodous Crustaceans,' in Messrs. Goodsir's "Anatomical and Pathological Observations."

† This fact may help to explain the phenomenon of 'protracted gestation;' for if at the

Spermatozoa are usually rendered irregular, and are more speedily brought to a close, by the admixture of fresh water with the spermatic fluid, which diminishes its density and alters their hygroscopic relations to it; but the admixture of animal fluids of somewhat higher density, such as milk, mucus, serum, or saliva, produces very little effect. The admixture of salt-water, again, scarcely affects the movement; nor does that of fresh, in the case of those animals whose ova are fertilized by the diffusion of the seminal fluid through it, as happens in many fresh-water Bivalve Mollusks. All such chemical agents as affect the chemical composition of the Spermatozoa, speedily put an end to their movements; and this result is instantaneously brought-about by an electric discharge, although a galvanic current does not seem to have any effect upon them. A higher or a lower temperature than that habitual to the organisms within which they are produced, usually seems to have a retarding influence; but the motions of the spermatozoa of Frogs and Fishes have been seen to continue, when the surrounding medium was beneath the freezing-point: and those of certain fresh-water Gasteropoda have not been arrested by contact with water of 158°—176° Fahr.

522. The mode of development of the Spermatozoa, as first discovered by Wagner, and since more fully demonstrated by Kölliker, is usually as follows.—In the parenchyma of the spermatic organs of some animals, but more commonly in the cavities of tubular vesicular organs, resembling ordinary glands in structure, and designated as *Testes*, there are formed certain large cells, which seem to correspond with the epithelial cells that have been shown to be the agents in the secreting process (§ 401). These primary cells,—corresponding with the primary cells within which the real sperm-cells are developed in the Ferns (Fig. 210, C), and with the 'primary cells of the pollen' in the Phanerogamia (§ 503),—give origin in their interior to a variable number of *vesicles of evolution*, each of which produces a single spermatozoon. The earliest stages of the development of the spermatozoon have not as yet been made-out; for on the one hand, the vesicle is filled with granular matter which obscures its other contents; whilst on the other, the spermatozoon itself does not exhibit those sharp distinct contours, dependent upon its high refractive power, which afterwards distinguish it. Gradually, however, the granular matter disappears, and the spermatozoon is distinctly seen lying coiled-up within its vesicle. When this is completely matured, it bursts, and gives exit to the contained spermatozoon; and if the primary cell have previously burst, as usually happens in Mammalia, the spermatozoa henceforth move freely in the spermatic fluid. In Birds, however, it is more common for the primary cells to continue so long unruptured, that, when the spermatozoa are set free from the vesicles of evolution, they are still contained within the enveloping cyst, usually straightening themselves out and lying in bundles; and it is only when the containing cyst at last ruptures, that these bundles are broken-up, and the individual spermatozoa dispersed.—The foregoing may be considered as the most complete mode of evolution of the

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time when sexual intercourse takes place, no ovum be prepared for fertilization, but the spermatozoa can retain their vitality for one, two, or three weeks, so as to fertilize an ovum matured at the end of that period, the usual term between *intercourse* and *parturition* will be extended by that interval, without any extension of the term between the actual *conception* and *parturition*.

spermatozoa; and it is on this type, that the process is most commonly performed. According to Wagner, however, vesicles of evolution are not always produced within the primary cells; but the nuclei of these may at once resolve themselves into spermatozoa, which then present a solid massive form, as in the Chilopoda, Acarida, and Entomostraca; or, as in the Nematoid Entozoa, the spermatozoon is formed by the conversion of the cell-membrane as well as of the nucleus of the primary cell. Even where the spermatozoon is formed within its own secondary cell or 'vesicle of evolution,' it is probably by the metamorphosis of its nucleus that it is really evolved; the process, so far as it can be traced, being extremely analogous to that by which the peculiar stinging organs of the Medusæ and Hydroid Polypes are developed, each of them being a cell whose nucleus is transformed into a fibre, which afterwards projects from one extremity of it by the rupture or solution of the cell-wall.

523. That the Spermatozoa are the essential constituents of the seminal fluid, and that the latter has not in itself any fertilizing power (which some have attributed to it), may now be regarded as fully proved. There are some cases, as pointed-out by Wagner, in which the 'liquor seminis' is altogether absent, so that they constitute the sole element of the semen; whilst, on the other hand, they are never wanting in the seminal fluid of animals capable of procreation. Moreover, there are many animals in which the fecundation of the ovum only takes place after the diffusion of the seminal fluid through water; and it is difficult to imagine that the liquor seminis, in so extremely dilute a condition, can be operative for its fertilization; although, when the vast multitude of spermatozoa discharged at once in such cases is borne in mind, and their power of continued spontaneous movement is taken into account, it seems obvious that a special provision has been made for bringing the spermatozoa and ova into direct contact. Such contact we have every reason to believe to be essential to the act of fecundation. The experiment was long ago tried by Spallanzani, and by Prevost and Dumas, and has been more recently repeated by Mr. Newport, of separating the spermatozoa from the liquor seminis by filtration, and of trying their respective effects upon the ovum. Mr. Newport found that when thus separated, and applied to different sets of eggs, those with which either the spermatozoa or the filtering-papers had been placed in contact, were almost universally fertilized, while only a very few of those treated with the liquor seminis were fecundated; and the fertilization of these last is attributed by him, with great probability, to the passage of a few of the spermatozoa through the filtering-paper.*

524. The development of the Spermatozoa is in most cases *periodical;* Man and some of the domesticated races being the only animals in which there is a constant aptitude for procreation. The spermatic organs, which remain for long periods in a state of atrophy, at particular times take-on an increased development, and their product is then formed in great abundance. Some of the most remarkable examples of this kind are presented by the class of Fishes; but the contrast is scarcely less notable in the Passerine Birds, whose testes in spring attain to twenty or even thirty

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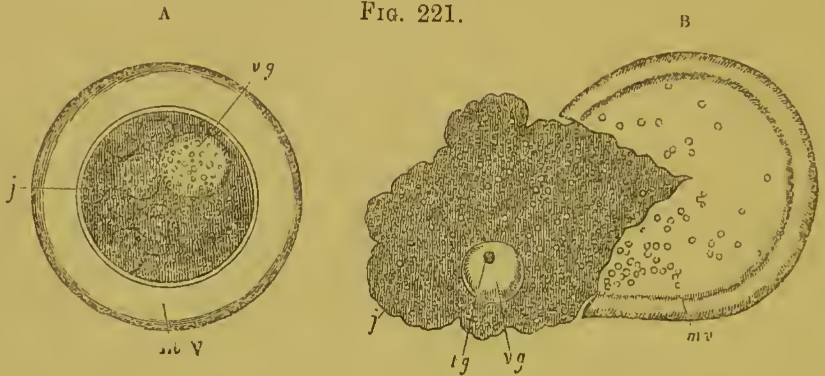
* "Philosophical Transactions," 1851, p. 204.—For the most recent and complete information on the Development and Varieties of the Spermatozoa, see the Art. 'Semen' by Drs. Wagner and Leuckart, in "Cyclop. of Anat. and Physiol.," Vol. III.

times the size and weight which they possess in the winter. It is when the organs are undergoing this rapid increase, that the several stages in the development of the Spermatozoa may be most advantageously studied.

525. The sperm-cell and its contents having been thus described, the 'Germ-cell' next presents itself for our consideration. It can scarcely be doubted that this is the real character of the *germinal vesicle* (Fig. 221, *v g*), which is a peculiar cell, with a very well-marked nucleus, termed the *germinal spot* (*t g*), that presents itself in every Ovum when matured for fecundation. It is surrounded by a mass of nutrient matter, chiefly composed of albumen and oil-particles, which is known as the *vitellus* or *yolk* (*j*); and the whole is enclosed within an envelope, which is termed the vitelline membrane or yolk-sac (*mv*). This membrane in the Mammal (whose ovum is here represented) is of peculiar thickness and transparency, and is distinguished as the *Zona pellucida*. The size of the ovum depends mainly upon the quantity of yolk which it contains; and this seems proportioned to the grade of development which the embryo is to attain, whilst still dependent upon it. Thus in the Insect, whose larvæ come forth from the egg in a very immature condition, the yolk is very minute, and the bulk of the larva on its immersion bears a marvellously small proportion to that which it soon presents. On the other hand in Birds, whose entire development into the ornithic type is accomplished before quitting the egg, the store of yolk is much larger in comparison, and the young is not nearly so disproportionate to the adult in size. After it has passed-forth from the ovarium, and has been fertilized, the proper ovum of many animals receives an additional investment of albumen, which is known as the 'white' of the egg; this is gradually drawn into the yolk as the latter is exhausted, and contributes to the nutrition of the embryo during the latter stages of its development. The ovum of Mammalia, whose yolk is extremely minute, does not (as might be supposed) constitute an exception to the principle just stated; for the embryo makes but a very small advance in development, whilst sustained by the material supplied by the yolk; and is dependent for support, during the whole remainder of its evolution, upon the nutriment which it derives from the parent by the more direct connection subsequently formed (§§ 607—608).

Fig. 221.



Constituent parts of *Mammalian Ovum*:—A, entire; B, ruptured, with the contents escaping; —*m v*, vitelline membrane; *f*, yolk; *v g*, germinal vesicle; *t g*, germinal spot.

526. The Development of the ovum, like that of the spermatic cells, sometimes takes place in the parenchyma of the germ-preparing organs or ovaries, sometimes within their cavity. In many of the lower animals, the testes and ovaries bear such a close resemblance to one another, as to be quite undistinguishable; and the same is the case in the early condition of the generative apparatus even of Man. In Articulated and Molluscous animals generally, the ovaries, like the testes, have a glandular character; but while the former retain the vesicular type, the latter are often prolonged into convoluted tubes. In the Vertebrata, we have a return to the parenchymatous type of ovarian structure; the ova being evolved in the midst of a very solid fibrous tissue or stroma. Each ovum seems to be developed within a 'parent-cell' of its own, which is called the *ovisac;* and the production of the ovisacs may take place very early in life, for in the ovaries of some animals they can be detected almost as soon as these organs are themselves evolved, and generally present themselves not long afterwards. The germinal vesicle is the part of the ovum which earliest shows itself within the ovisac; and is at first seen in its centre, surrounded by an assemblage of granules which is the commencement of the yolk. This collection gradually augments, and the vitelline membrane is developed around it; and as the ovum advances towards maturity, it draws from the enveloping vascular substance, that amount of albuminous and oleaginous matters which is appropriate to it. Like the augmented development of the contents of the spermatic organs, that of the ovaries is generally periodical; a large number of ova, in most of the lower tribes of animals, are advancing towards maturity at the same period, and they are discharged either simultaneously or successively; after which, the ovarium relapses into its previous inactivity. In the Human female, however, and in that of many domesticated animals, the difference between these two states is much less marked; and although the complete maturation of the ova, and their escape from the ovary, may only take place at particular intervals, yet there appears to be a continual advance towards that maturation, even during the earlier periods of life. When it has attained its full development, the ovum escapes from the ovisac, which either ruptures or thins-away to give it exit; and it is then ready for fecundation. If *not* fecundated, it usually dies within a few days; its continued life being dependent upon the due performance of the operations for which it is destined.

527. The Fecundation of the ovum is accomplished by the contact of the spermatozoa; and the place and circumstances of this contact vary considerably, as already pointed-out. It does not appear, however, that the essential nature of the fecundating process is in any way influenced by the locality in which it occurs; and what is true of one case, is probably true of all. Great difficulties, however, stand in the way of the determination of the changes in the ovum, which immediately precede and follow the act of fecundation; and observers are by no means agreed upon the point. The 'germinal vesicle' of the ovum which is approaching maturity, no longer presents its ordinary pellucidity, but becomes obscure; and this obscuration, which has led some to the belief in its entire disappearance, is affirmed by Dr. Barry to be due to the development of a mass of cells in its interior, which sprout, as it were, from the germinal spot, and gradually fill-up its cavity. This statement is confirmed by

Wagner, and Vogt; whose observations lead them to the belief that, when thus filled with cells, the germinal vesicle bursts and sets them free, so that they become diffused through the yolk. This view is adopted also by Mr. Newport, as the result of his recent observations on the ovum of the Amphibia; and he states that this dissolution of the germinal vesicle and diffusion of its contents take place as a preparation for fecundation, and not in consequence of it.* That the spermatozoa actually make their way through the vitelline membrane, and penetrate to the interior of the ovum, has been affirmed at different times by various observers (as MM. Prevost and Dumas, Dr. Martin Barry, Prof. Wagner, Dr. Nelson, and Dr. Keber); but exceptions having been taken to their statements by other eminent physiologists,† they have not obtained general currency. The results of the very careful study of the process of impregnation in the Frog, recently made by Mr. Newport, seem, however, to leave no reasonable doubt on this point: for the penetration of the spermatozoa into the thick gelatinous envelope of the ovum, so that their large extremities come into close contact with the vitelline membrane, may be observed (as the Author can himself bear testimony) without any difficulty, and under favourable circumstances, the spermatozoa may be detected *within* the vitelline cavity in direct communication with the substance of the yolk.‡ They do not enter by any special orifice, but pierce the substance of the envelopes at any part with which they may happen to come into contact. Some time after entering the yolk-chamber, they become disintegrated; being resolved at first into elementary granules, and probably afterwards deliquescing entirely. It appears from Mr. Newport's ingenious experiments, that the contact of a single spermatozoon is not adequate to produce complete fecundation, but that the penetration of a certain number of spermatozoa is requisite; and he has ascertained that fecundation may be effected *partially* (so as to occasion *some*, though not all, of the normal changes in the ovum), by a smaller amount. Availing himself of the agency of caustic potass, which had been ascertained by Frerichs to be a powerful solvent of the spermatozoa, he applied this agent to the ova at determinate periods after the application of these bodies; and he found that when the interval of time between the application of the seminal fluid and that of the solution of potash was only one or two seconds, the 'segmentation' of the yolk took place (§ 528), but no embryoes were produced. When, however, the interval was five seconds, a very few embryoes were formed; but when the interval was fifteen or more seconds, they were produced in greater number.—The spermatozoon may be looked-upon as a sort of solidification of the contents of the 'sperm-cell,' endowed with a temporary power of spontaneous movement, for the purpose of bringing it into contact with the 'germ-cell,' and resolved by that contact into its original fluid form, in which it is capable of acting upon the product of the germ-cell within the ovum. It is obvious that the whole process thus comes to bear a very close correspondence to the fertilization of the embryonal vesicle, by the antherozoids of Cryptogamia, or by the pollen-tubes of Flowering-Plants.

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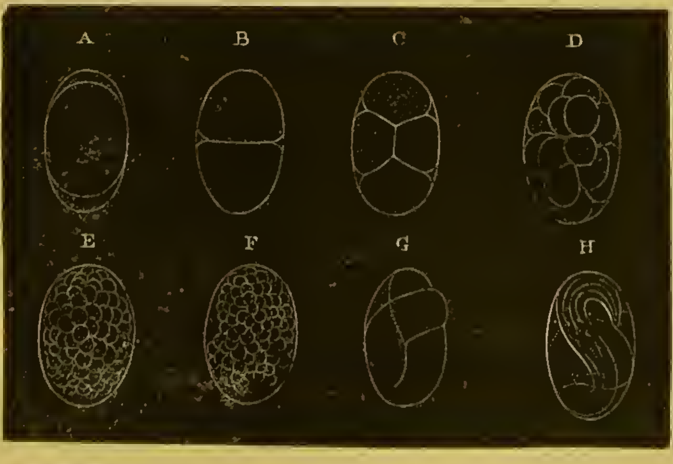
* "Philos. Transact.," 1851, p. 179.

† See especially Dr. Bischoff's "Widerlegung des von Dr. Keber bei den Najaden, und Dr. Nelson bei den Ascariden, behaupteten Eindringens der Spermatozoiden in das Ei," Geissen, 1854.—Dr. Bischoff most completely disposes both of Dr. Keber's and Dr. Nelson's assertions, and fully points-out the errors of observation and of interpretation, on which they have been based.

‡ "Philos. Transact.," 1853, pp. 266—281.

528. The first changes consequent upon fecundation are so nearly the same in their character in all Animals, that it is desirable to give such a general account of them, as shall be applicable to the greater number of individual cases, and shall thus serve as a foundation on which to build the special descriptions hereafter to be given, of the principal plans of development which are exhibited during the later stages. In the impregnated ovum of many Entozoa, whose transparency enables their interior to be more clearly discerned than that of most higher animals, a new and peculiar cell, the 'embryonic vesicle,' is seen in the midst of the yolk; which, from its subsequent history, may obviously be regarded as the equivalent of the 'primordial cell' of Phanerogamia (§ 505). The origin of this cell has not been distinctly traced; but it is probably formed *de novo*, like the primordial cell of the Vegetable embryo, either as a 'free cell' or in the interior of one of the secondary cells that have been set-free by the rupture or diffluence of the germinal vesicle. The latter would seem most probable, from the analogy of the Phanerogamia. In the ova of certain *Entozoa* (as *Cucullanus* and *Ascaris dentata*), and perhaps in those of other animals belonging to the inferior classes, the development of the embryonic mass commences very much after the same plan as in Plants. The primordial cell lying free in the midst of the yolk, subdivides into two, each of these into two others, and so on, according to the regular type of cell-multiplication in a growing part; so that, in place of the single cell, we have first 2, then 4, then 8, then 16, then 32, and so on. As these cells multiply and enlarge, they draw into themselves the nutrient matter which surrounds them; so that, when the whole yolk has been thus absorbed, the yolk-bag is entirely occupied by the embryonic mass, entirely composed of cells evolved from the primordial embryo-cell, thus representing, in the manner of its development, the embryo of a Leguminous plant (§ 506). But in other Entozoa (even in some species

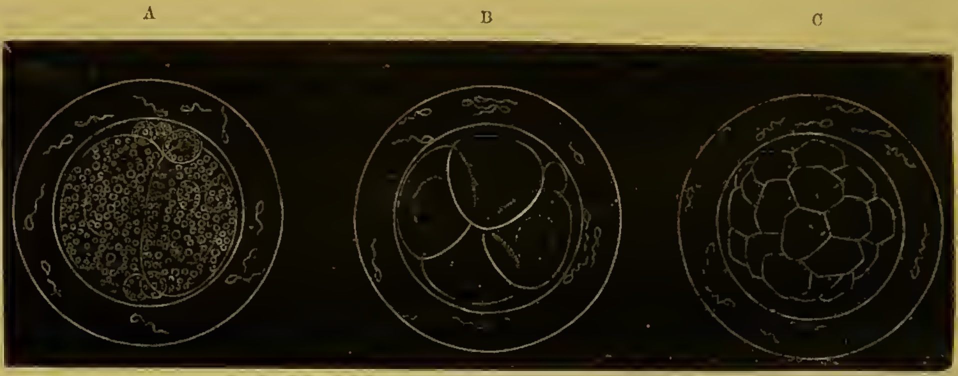
Fig. 222.



Successive stages of Segmentation in the vitellus of the Ovum of *Ascaris acuminata*:—A, ovum recently impregnated, the yolk-bag slightly separated from the enveloping membrane: B, first fission into two halves; C, second fission, forming four segments; D, yolk, now divided into numerous segments; E, formation of 'mulberry mass' by further segmentation; F, the mass of cells now beginning to show the form of the future worm; G, further progress of its evolution; H, the worm, formed by the conversion of the yolk-cells, now nearly mature.

of *Ascaris*) a different plan is followed; for each of the cells which is produced by the successive fissions of the embryonic vesicle, draws around itself a certain portion of the yolk, which thus successively divides into as many segments as there are embryonic cells; and thus is produced that *segmentation* of the entire yolk, or of a part of it, which is one of the most striking features in the early history of embryonic development in all the higher animals. The several stages of this process, as it takes place in the ovum of *Ascaris acuminata*, are shown in Fig. 222, A, B, C, D, E; and, for the sake of comparison, the early stages of segmentation in the yolk of the *Mammalian* ovum are shown in Fig. 223, A, B. C. It should be stated, however, in regard to the latter, that the primordial cell has not yet been clearly made out in its interior, and that the nature of the body which forms the centre of each segment has not been precisely determined; if not actually a cell, however, there can be little doubt that it is a cell-nucleus, and that it is the lineal descendant of the immediate product of the mutual action of the contents of the 'sperm-cell' and 'germ-cell.'

FIG. 223.

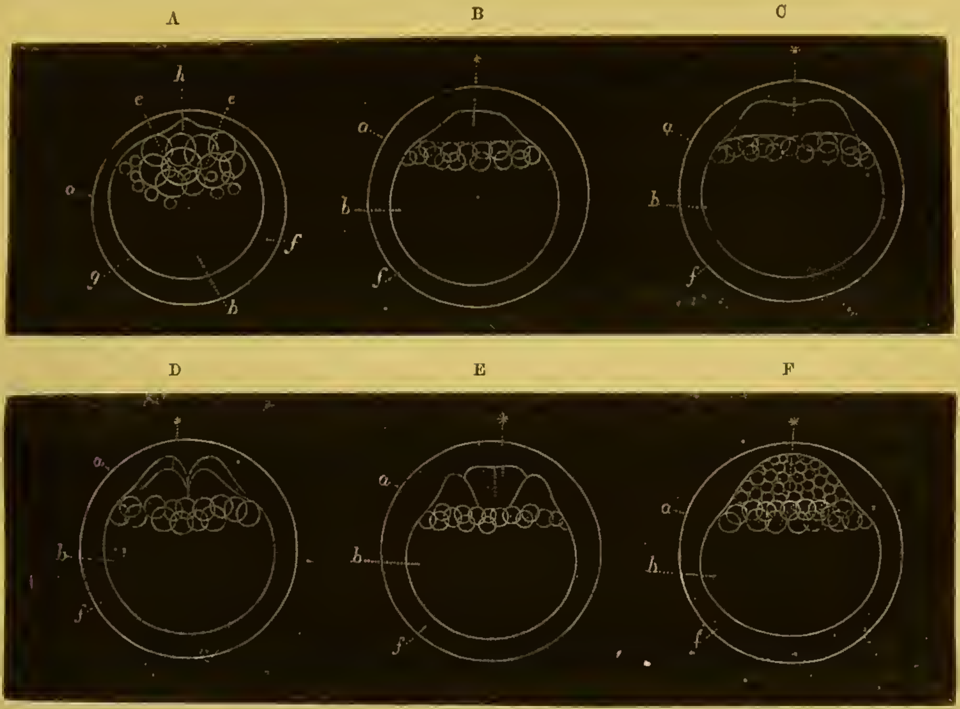


Progressive stages in the Segmentation of the vitellus of the *Mammalian* Ovum:—A, its first division into two halves; B, subdivision of each half into two; C, further subdivision, producing numerous segments.

529. When this process has gone-on to such an extent, as to fill the entire yolk-bag with an aggregation of minute spherical segments of yolk (Fig. 222, E), having each a minute cell or cell-nucleus in its interior, every segment becomes invested with a cell-membrane of its own; so that the result produced is in effect the same, as in the case in which the descendants of the embryonic vesicle drew the yolk into their own cavity; for the yolk-bag is now occupied by a mulberry-like mass of cells, every one of which has a share of the 'germinal capacity' possessed by the original embryonic vesicle; and it is by the transformation of these cells, that the embryonic structures are subsequently evolved.—In a considerable number of the higher animals, however, in whose ova the yolk is large enough to carry-on their development, so that they arrive at their characteristic forms while yet within the egg, this segmentation does not take place in the whole yolk, but only in that part of it immediately surrounding the embryonic vesicle, which lies on the surface, instead of in the centre, of the yolk. This may be well observed in Fishes (Fig. 224, A-E); and according to M. Coste, it is by a similar process that the *cicatricula* or germ-spot is produced at the surface of the yolk-bag of Birds, whence all subsequent changes emanate. This separation of the

yolk into two parts—that which cleaves, and that which does not cleave, —has not yet been observed in any Invertebrata, save the Cephalopoda.

Fig. 224.



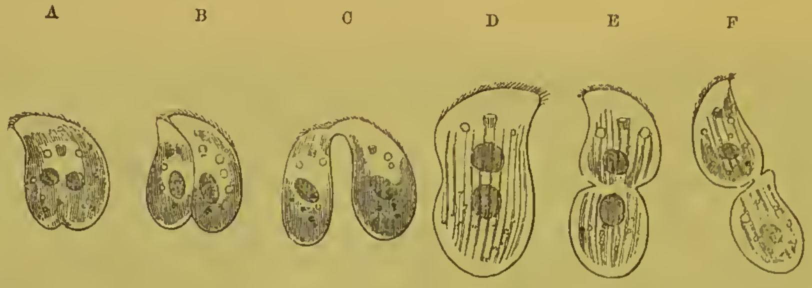
Early stages in the development of the Ovum of *Coregonus palæa.* In all the figures, *a* indicates the shell-membrane; *b*, the vitellus; *e*, *e*, oil-globules in the vitellus; *f*, the albumen; *g*, vitelline membrane; *h*, situation of the germinal vesicle; *, germinal mass:—A, ovarian ovum, with a slight elevation in the situation of the germinal vesicle; B, ovum two days after fecundation, showing the germinal elevation, probably produced by the attraction of a portion of the yolk around the embryonic vesicle; C, ovum rather more advanced, showing the furrow indicative of the first cleavage; D, later stage, a second cleavage having taken place, so as to produce four segments; E, further progress of the segmentation; F, development of the 'mulberry-mass' by continued fission.

It is obvious that the non-cleaving portion of the yolk is to be regarded as a superaddition to the true yolk, which is employed in forming the 'mulberry mass,' being destined to afford the material for the ulterior development of the cells of which this is composed; the former may be distinguished as the 'food-yolk,' the latter as the 'germ-yolk.'

530. The most general phenomena of Reproduction having been thus described, we have now to turn our attention to the principal specialities which the process exhibits in the several groups of the Animal kingdom. —Of the history of reproduction among the *Protozoa,* our knowledge is at present very limited. The propagation of the greater number of the (so-called) Polygastric *Infusoria* is only known to be effected by the process of subdivision, or *fissiparous* multiplication (Fig. 225), which is analogous, on the one hand, to that which we have seen to prevail in the parallel group of Plants (§ 349), and on the other to that which occurs in the earliest stage of embryonic development in the highest Animal (§ 528). It is curious to observe that the direction of this division is not constant in different individuals of the same species; this being sometimes longitudinal (A, B, C), sometimes transverse (D, E, F). It is possible that there may be here some such alternation, as we commonly see in the direction

of the subdivision of cells, which remain connected together and are not growing in one direction only (Fig. 165, E). The multiplication of

FIG. 225.



Fissiparous multiplication of *Chilodon cucullulus*; A, B, C, successive stages of longitudinal fission; D, E, F, successive stages of transverse fission.

'zöoids' may take place after this method with such extraordinary rapidity, that, according to the computation of Prof. Ehrenberg, founded upon observations made on *Paramœcium,* no fewer than 268 *millions* of these Animalcules might be produced in a month from a single one.—Besides the fissiparous mode, the *gemmiparous* is not unfrequently seen, a bud being put forth, which gradually increases in size, acquires the characters of its stock, and at last becomes detached; this is especially observable in the *Vorticellinæ* (Fig. 226), which, in their stationary habits, strongly remind us of Polypes, whose gemmiparous tendency is so remarkable.—In addition to these methods, it would appear that certain Infusoria, especially the *Kolpodinæ,* propagate by the breaking-up of their own mass into reproductive particles; a method that strongly reminds us of the dispersion of the zoospores of such Algæ as the *Achlya prolifera* (Fig. 164). But it can scarcely be doubted that, as this method of multiplication is in reality only an extension of the same primordial stock, a true *generative* act must occasionally become necessary, in order to reproduce the capacity for such continued propagation. It is not an unimportant consideration bearing upon this subject, that the appearance of Animalcules in fluids, into which it seems certain that their germs must have been conveyed by the air, indicates that they must have arrived there in some different condition; since most of these Animalcules are themselves killed by desiccation, although the more highly-organized Rotifera may be wafted by the atmosphere, and dispersed over the entire globe, in a perfectly dry state, without the loss of their vitality. There is certainly much still to be learned respecting these remarkable beings; and nothing but patient observation of particular species, extending over long periods of time, will unravel the mystery which at present hangs over their nature and origin.—It might be expected, from the analogy of the Protophyta, that a process resembling 'conjugation' would now and then occur in the Protozoa; and such a process has been remarked by Prof. Kölliker and Dr. Cohn in *Actinophrys.** Two *Actinophrys* approximate and coalesce, so as to form what appears to be a single individual; but the nucleus of this developes itself into a cell, which gradually takes-on the character of its parent; and the young Actinophrys thus generated probably soon escapes from the body which encloses it. A like process has been observed by Prof. Stein to take place in *Gregarina*, a single-celled Entozoon inhabiting the intestinal canal of many of the lower animals; for two of these bodies fuse by conjugation into one sphere, which acquires a distinct integument or cyst; a great part of their contents becomes converted into spindle-shaped 'spores,' whilst the remainder liquefies; and the spores set-free by the bursting of the cyst, seem to develope themselves into a new generation of Gregarinæ.*

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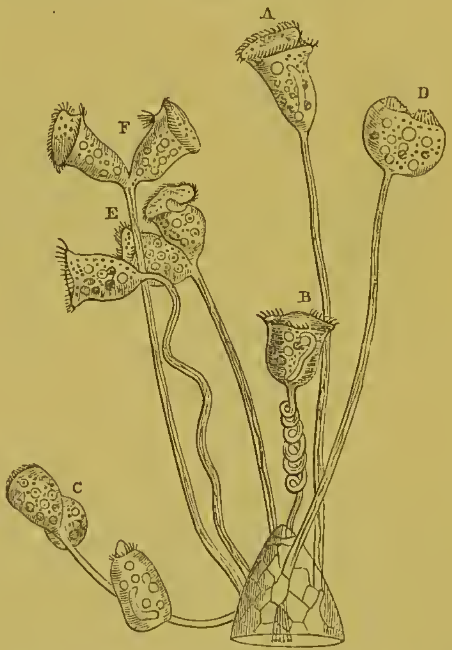
* "Siebold and Kölliker's Zeitschrift," 1849 and 1851.

531. It would be premature, however, to assert that such is the ease with every reputed species of Infusoria; and it appears to have been well established by Prof. Stein's observations, that, in certain instances at least, one form originates in another very dissimilar to it,—as had, indeed, been frequently suspected from the fact of the occasional disappearance of particular tribes of Animalcules from infusions that previously swarmed with them, and from their replacement by others of very different aspect. The *Vorticellæ* (which are bell-shaped Animalcules attached by stalks, and having a fringe of cilia disposed around a disk, Fig. 226), are seen at a certain stage of their existence to become 'encysted;' drawing-in their ciliated disk, and contracting their bodies into a ball; at the same time secreting around themselves a gelatinous mass, which solidifies into a firmer elastic covering. This process sometimes takes place while the Vorticella is attached to its stalk (Fig. 227, A); but the stalk in that case soon breaks; and more commonly the cyst is formed around the animal whilst it is freely swimming (B). These encysted Vorticellæ may undergo two sets of changes very different in kind. In some, the band-like nucleus (A, *b*) breaks-up into a number of disciform bodies (C); and these grow at the expense of one part of the granule-substance of the original animalcule, whilst the other part becomes changed into the clear gelatinous mass, in which the embryoes afterwards swim. The original Vorticella-vesicle at this period presents a sacculated aspect (D), and many hyaline spaces are seen, which sometimes disappear suddenly, to reappear elsewhere. Finally, the cyst ruptures, and the gelatinous mass with its included embryoes is discharged (E); these have a simple monad-like form, and so closely resemble in their appearance and movements the smallest and youngest Vorticellæ yet observed, that

FIG. 226.



Group of *Vorticella nebulifera*, showing A the ordinary form, B, the same with the stalk contracted, C, the same with the bell closed, D, E, F, successive stages of fissiparous multiplication.

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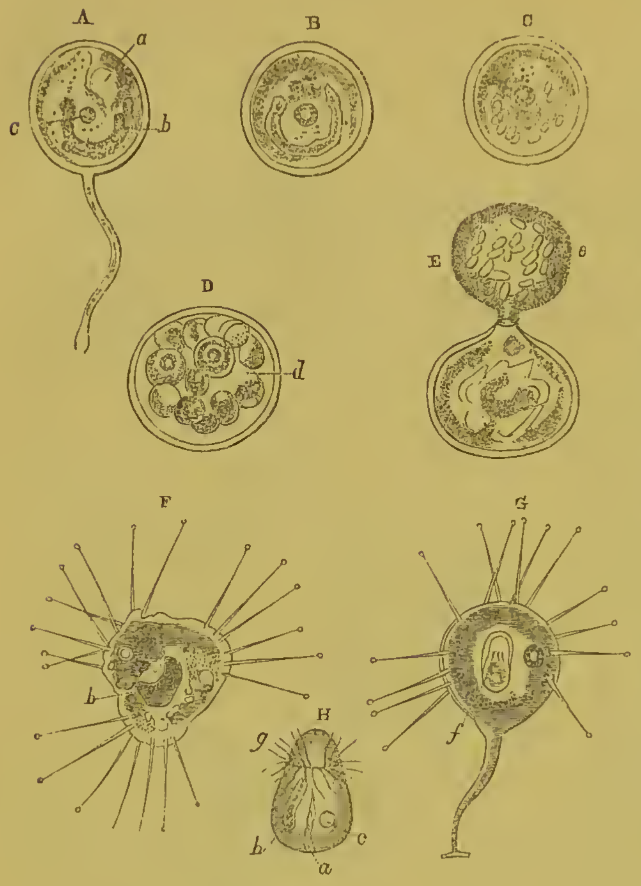
* Op. cit., Band III., Heft 4.

it can scarcely be doubted that they are directly developed into the form of the body from which they were given-forth. In other instances, however, the encysted Vorticella becomes changed into an *Acineta* (a form closely resembling that of *Actinophrys sol*), by extending itself, sometimes on one side, sometimes on all sides, and by thrusting-out processes of its wall thus thinned (F); whilst its band-like nucleus becomes entirely metamorphosed into a free body of ovate form, which carries at its more pointed end a circlet of long vibrating cilia, while its more obtuse end is perforated by a mouth which communicates with a distinct oral cavity (G). In the interior of this offspring we already observe a long, oval, slightly-bent nucleus, and a round rhythmically - contracted clear space; and its whole aspect is that of a young Vorticella-bud just ready to quit its stock. This body escapes from the interior of the Acineta, by a gap formed in some part of its wall; which soon closes again; and the Acineta then goes on stretching-out and retracting its radiating filaments, and after a time produces in its interior a new nucleus for a second Vorticella-bud.*—It would seem most probable from the analogy of *Actinophrys* (§ 531), that the latter of these processes is consequent upon the conjugation of two individuals, and is therefore a true generative act; while the former seems rather to correspond with the evolution of 'zoospores' in *Protophyta* (§ 351), or with that of free gemmæ in the Cystic state of the

Fig. 227.



Development and Metamorphoses of *Vorticella microstoma*:—A, full-grown individual in its encysted state; *a*, retracted oval circlet of cilia; *b*, nucleus; *c*, contractile space;—B, a cyst separated from its stalk;—C, the same more advanced, the nucleus broken-up into spore-like globules;—D, the same more developed, the original body of the Vorticella, *d*, having become sacculated, and containing many clear spaces;—E, one of the sacculations having burst through the enveloping cyst, a gelatinous mass, *e*, containing the spores, is discharged;—F, transformation of encysted Vorticella (B) into form of *Acineta; b*, nucleus;—G, stalked Acineta-form of Vorticella, enclosing a young one, the result of the transformation of the nucleus;—H, young free Vorticella; *a, b, c*, as in Fig. 1; *g*, posterior circlet of cilia.

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* See "Siebold and Kölliker's Zeitschrift," Band III., Heft 4; and the translation of Prof. Stein's Memoir in "Annals of Nat. Hist.," 2nd Ser., Vol. IX., p. 471. See also M. Jules Haime on *Trichoda lynceus*, in "Ann. des Sci. Nat.," 3e Sér., Zool., Tom. XIX., p. 109, *et seq.*

Cestoid Entozoa (§ 571). In their encysted state, the Vorticellinæ appear to be capable of undergoing desiccation without the loss of their vitality; and the same is probably true of other Animalcules.

532. Although our knowledge of the Generative process in the *Porifera* (Sponges) is very incomplete, yet there can be little doubt that it is conformable, in all essential particulars, to the ordinary type. Between the cortical and the central substances of *Tethya*, Mr. Huxley has detected ova, with their characteristic vitellary membrane, yolk-substance, germinal vesicle and germinal spot; while the granular mass in which these are imbedded, consists entirely of small circular cells about 1-3000th of an inch in diameter, and of spermatozoa in every stage of development from those cells. It is remarkable that the ova are here in no way separated from the spermatozoa, but lie in the spermatic mass like eggs packed in sand.*—Two classes of reproductive bodies have been observed in Sponges; namely, *gemmules*, and *capsules*. The former seem like detached portions of the gelatinous flesh lining the canals, which, being furnished with cilia, issue-forth from the vents, and transport themselves to distant spots where they may lay the foundation of new sponges. The latter are bodies of a larger size, frequently having a very peculiar investment strengthened by siliceous particles, and containing numerous globular particles, every one of which, when set-free by the rupture of its envelope, may become a separate zooid. It seems probable that these capsules are, like the spore-cases of Mosses, true generative products; and that the globular bodies then set-free, may represent the component cells of the 'mulberry mass' resulting from the segmentation of the yolk, which, in these very simple forms of animal existence, may separate from each other, and may develope themselves into independent 'zooids,' just as the spores of the Moss, which are the immediate descendants of its primordial cell, develope themselves into separate 'phytoids' (§ 491). The view of the relation between the gemmules and the capsules, which regards the former as free gemmæ, and the latter as the true ova, is in harmony with the fact, that while the former are produced at the period of the most active growth of the sponge; the latter are developed (like the ova of the Hydra, § 533) towards winter, when the nutritive operations are failing, and when in many cases the parent-structure is about to die.—Of the history of the *development* of sponges, very little is yet known; but as it appears from the observations of Mr. Carter,† that the germinal particles set-free from the capsules of Spongilla give origin directly to protean-cells, resembling those of which the great mass of their tissue is composed, it may be surmised that the process is of the simplest kind, consisting in the multiplication of these protean-cells by duplicative subdivision, and in the production of the component spicules of the skeleton within some of these; the aggregate mass, as it is thus evolved, taking the characteristic form of the species.—Of the nature of the Generative process in the allied group of *Rhizopoda*, nothing whatever is known. It may be stated with certainty, however, that those composite fabrics, which constitute the in-

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* "Ann. of Nat. Hist.," 2nd Ser., Vol. VII., p. 370.—Each spermatozoon is described by Mr. Huxley as being not developed within its sperm-cell, but as being itself the sperm-cell, metamorphosed by the protrusion of a long filament which becomes the 'tail,' whilst the remainder, somewhat elongated and pointed, forms the 'head.'

† Op. cit., Vol. IV., p. 89.

teresting group of *Foraminifera*, are the result of gemmation from a single stock, each chamber of their polythalamous cells being the product of a distinct zooid. The successive zooids are put-forth according to a definite pattern, which is tolerably constant for each species; and their mutual independence is shown by the continuance, not merely of their existence, but of their power of increase, after their detachment from each other.

533. In the class of *Polypifera*, the true Generative operation is universally performed; notwithstanding that the multiplication of independent zooids is still effected to a great extent by the process of gemmation. The *Hydra* presents us with almost the simplest possible condition of their sexual apparatus, no special organs being developed for the evolution of either the sperm-cells or the ova, which are formed in the substance of the wall of the stomach;* but they are not evolved indiscriminately in every part, the former being always found just beneath the arms, and the latter nearer to the foot. Although both sets of generative organs may be developed in a single Hydra, yet it is not uncommon for one to bear sperm-cells only, and for another to produce only ova. Whether the Hydræ be monœcious or diœcious, however, it is probable that the fertilization of their ova is accomplished by the diffusion of the spermatozoa through the water, rather than by any more direct application.—The development of the ovum has not yet been studied; but there can be little doubt that the embryo is at once evolved into the likeness of its parent, since the collections of fresh water inhabited by the Hydra do not contain any organism that could be regarded as an intermediate form. It seems probable, therefore, from the analogy of other cases (§ 538), that when the yolk-bag has been filled by the mulberry-mass, the cells of the interior liquefy, so as to leave a cavity which becomes the stomach, whilst the cells of the exterior remain to form the walls of that cavity, and absorb its contents;—that a thinning-away takes place in a certain spot of this wall, so as to form the mouth, as happens, in fact, during the development of the gemmæ which bud-off from the body of the adult Hydra (Fig. 228);—and that, as in those gemmæ, the tentacula are gradually developed around the mouth, making their first appearance as little knobs, and then progressively elongating themselves until they have attained their normal dimensions.† Although a multiplication of independent 'zooids' takes place in this simple Zoophyte to an unlimited extent, these are all but repetitions of the original form; and every one of them may in its turn develope a sexual apparatus, without the intervention of that intervening form, which, under some aspect or other, seems to be presented by all the other Hydroid Zoophytes (§§ 538—540).

534. The origination of a 'new generation' by the fertilization of an ovum, is, however, a rare phenomenon in the Hydra, in comparison with the multiplication of the existing generation by the process of Gemmation. The gemmæ which are to become independent 'zooids,' at first

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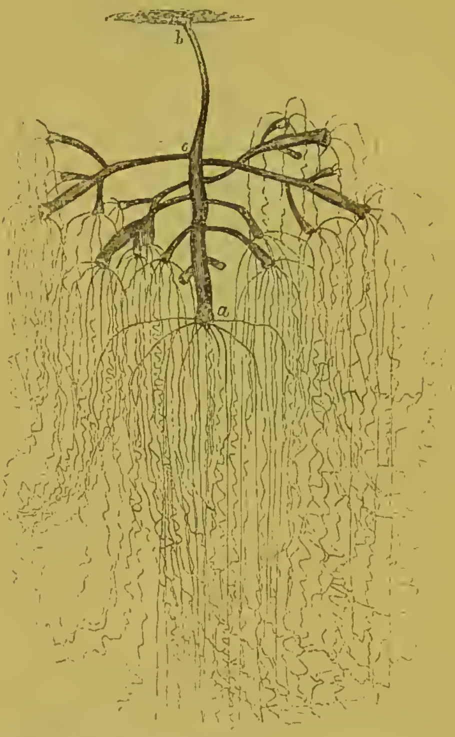
* According to M. Rouget ("Comptes Rendus de la Societé de Biologie," 1851, p. 141), the ova originate in an 'ovular mass' resulting from an increased development of the cells between the inner and outer layers of the polype. This mass may be considered as representing an ovisac; and the greater part of its cells disappear by diffluence, having apparently elaborated the nutrient material which is appropriated by the ovum.

† A particular description and figures of the sexual process in the Hydra, are given by Dr. Allen Thomson in the "Edinb. New Phil. Journal" for April, 1847.

appear as knob-like protuberances from the body of the original 'stock;' they gradually increase in size, and come to present something of its own form; an aperture is then seen at the free extremity, and around this tentacula begin to sprout. During this period, the cavity of the bud communicates with that of the stock, and the former is of course at first supplied with nutriment entirely by the latter; and even after the tentacula of the bud are sufficiently developed to enable it to obtain food for itself, the communication remains open for a time, as appears from the fact that either of the stomachs is distended when the other is fed. As the bud advances towards completeness, however, the aperture contracts, and is at last obliterated; the stalk itself, by which it is attached, gradually becomes more slender, and is at last broken by any slight effort on the part of either the Hydra or the gemma; and the latter, thus set free, henceforth leads a life of entire independence. Not unfrequently, however, if the weather be warm, and the supply of food be plentiful, the gemma itself begins to put forth secondary gemmæ before its separation from the stock; and thus a composite structure may be evolved, such as that represented in Fig. 228, in which there are ten primary buds in various phases of development, issuing from the central stock, and *nine* secondary buds proceeding from these.—This process of Gemmation seems to continue almost indefinitely, under the influence of warmth and food; and the determining condition of the occurrence of the true Generative operation is a diminution of temperature, which, threatening destruction to the parent, calls-forth the exercise of the special provision for the perpetuation of the race. In this we trace a marked conformity to the plan, of which we see very striking manifestations in the Vegetable kingdom; thus, it is observable of the fruit-trees of temperate climates, that under the habitual influence of a high temperature, and when copiously supplied with aliment, they will extend themselves by the formation of leaf-buds and branches, and will bear few flowers or even none; whilst, on the other hand, if the temperature be lowered, or a part of their supply of aliment be cut-off, the extension of the individual fabric will be checked, but it will bear a much larger quantity of flowers and fruit. (See also § 580.)

FIG. 228.

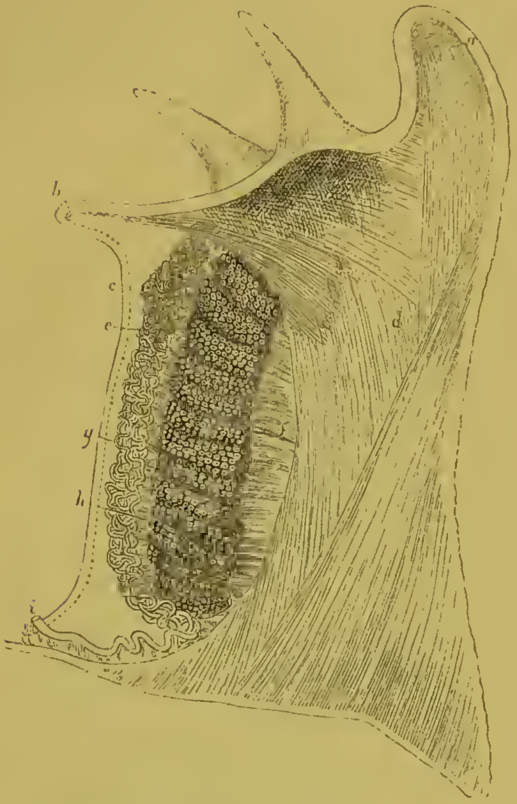


Hydra fusca in gemmation; *a*, mouth; *b*, base; *c*, origin of one of the buds.

535. A more specialized form of the Generative apparatus is seen in the *Helianthoid* and *Asteroid* Zoophytes; in which the spermatozoa and ova are developed in special organs that occupy the chambers surround-

ing the digestive cavity. There is, however, no external distinction between the *testes* in which the sperm-cells are evolved, and the *ovaries* which contain ova; and it is only by microscopic examination of their contents, that the real nature of these generative organs (which do not exist together in the same individuals) can be determined.* In the *Actinia coriacea* (Fig. 229, *e*), they are about two hundred in number, and form elongated masses attached along the inner border of the leaflets or vertical partitions (*d*), that radiate inwards from the outer integument (Fig. 35). Each testis or ovary is composed of several horizontal folds or plaits, which, when unfolded, show this body to be about three times the length it assumes when attached to the leaflet; and each plait is made up of two layers of membrane, between which the ova are developed. Where the sperm-cells or ova do not intervene, however, these two layers come into apposition, and form in the first place a kind of mesentery (*f*) by which the organs are attached to the leaflet; but they then separate, passing one on each side of the leaflet, so as to line the intervening spaces, and become continuous with the membrane lining the tentacula and digestive cavity, and through this with the external investment. Hence, notwithstanding the size and importance of the testes and ovaria, their structure is the simplest possible.†—The ova, set free by the thinning-away of the membrane which covers them, then lie

Fig. 229.



Interior of one of the ovarial chambers of *Actinia coriacea*, showing the Generative apparatus:—*a*, lip; *b*, border of mouth; *c*, wall of stomach; *d*, muscular partition; *e*, testis or ovary; *f*, mesenteric membrane connecting it to the muscular partition; *g*, vermiform filament containing filiferous capsules; *h*, membrane connecting it to the ovary; *i*, duct passing towards the stomach.

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* It has been supposed by many anatomists (the idea having been specially advocated by Prof. Wagner) that the 'vermiform filaments' so abundant in the ovarian chambers, are the testes of these animals. But it is now satisfactorily proved that the bodies which were regarded as spermatozoa by Wagner, are really the same peculiar 'threads' or 'darts' as are found in the 'filiferous' capsules of the skin of the Actiniæ. (See, for a detailed account of these curious bodies, Mr. Gosse's "Rambles of a Naturalist," pp. 432, 433.) That the organs previously designated ovaria, are really testes in about half of any number of Actiniæ, was first shown by Kölliker ("Beitrage zur Kenntniss der Geschlechtsverhältnisse und der Samenflüssigkeit der Wirbellosen Thiere," 1841) and Erdl ("Muller's Archiv.," 1841-2). An excellent account of the whole Anatomy of the Actinia is given by M. Hollard in "Ann. des Sci. Nat.," 3e Sér., Zool., Tom. XV.

† See the 'Anatomy of Actinia Coriacea,' by Mr. T. P. Teale, in the "Transactions of the Leeds Philosophical and Literary Society," Vol. I., part I.

freely in the ovarial chambers; and as they are usually retained in these cavities until they have passed through their early stages of development (though the grade which they have attained at the time of their discharge does not seem to be constantly the same), it is certain that they must there receive the fertilizing influence of the spermatozoa, which, escaping from the testes of the males, would be diffused through the surrounding water.—As far as the history of the embryonic development of the Helianthoid Polypes is yet known, it seems to be essentially as follows. The mulberry-mass, emerging from the egg-covering, acquires cilia upon its surface, by whose action it can be propelled through the water; it is known in this condition by the name of 'gemmule;' and in this phase of their development, the embryoes are frequently found in the interior of the tentacula. The cavity of the stomach and the mouth are formed by the process described in a preceding paragraph (§ 533); and the tentacula originate after the same fashion, a single row only being first produced, and new rows subsequently springing up. The wall of the stomach is seen to consist of a double membrane, of which the two layers are at first in contact; but a separation takes place between them, so that the inner, which forms the coat of the stomach, no longer remains connected with the outer, which constitutes the external integument, except by the vertical leaflets that divide the intervening spaces. The embryoes at last find their way into the stomach, by the orifice of communication between its cavity and the surrounding ovarial chambers; and they are discharged from the mouth, sometimes in considerable numbers at once. There seems reason to think that in the earlier phase of their development, they sometimes escape from the pores at the extremity of the tentacula.*—The mode in which the generative function is performed in the *Asteroid* Polypes, is the same in all essential particulars as that just described.

536. The process of extension by Gemmation is carried-on to an almost indefinite amount in the composite forms of these Zoophytes, the zooids usually remaining in more or less intimate connection with each other, as already explained (§§ 38, 152). It is seldom that the gemmæ spontaneously detach themselves, though they will maintain an independent existence if artificially separated; in the *Actinia lacerata*, however, according to Sir J. G. Dalyell (Op. cit., p. 229), this seems to be the regular mode of multiplication, the base of attachment spreading-out, and detaching little fragments of which every one may develope itself into a new Actinia. In the branching Corals, the multiplication of zooids is commonly effected by the duplicative subdivision of the entire body of the polype; and this subdivision is occasionally though rarely seen in the solitary Actinia (Op. cit., p. 221). No instance is known among these orders, in which the gemma developes itself into a form different from that of the stock which put it forth; nor does the embryo ever seem to assume any other type than that of its parent; but, whether produced by gemmation, or by the true generative operation, the new Polypes appear to have the same structure and endowments.

537. A very different succession of phenomena is presented, however, by *Compound Hydroida* (§ 151). These, looking only to their Nutritive

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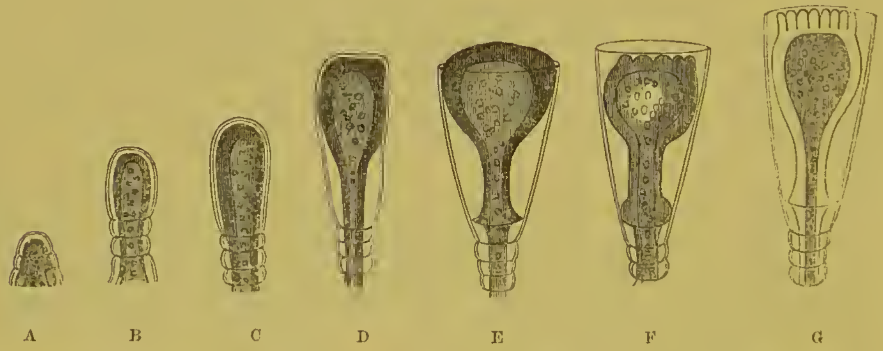
* On this subject, see especially Sir J. G. Dalyell's "Rare and Remarkable Animals of Scotland," Vol. II.; Chap. X.

apparatus, may be considered as not differing in any essential particular from a Hydra-stock, which has put-forth a set of primary and secondary gemmæ that have not yet separated from it (Fig. 228). But their Generation is carried-on upon a type altogether dissimilar: and the curious discoveries which have been made of late years, in regard to the mode in which it is accomplished, reveal a connection previously altogether unsuspected, between this group and that of *Acalephæ.*—It will be desirable, in the first place, to consider the relation which the polypes of one of these composite structures bear to each other and to the common stock. It will be recollected that the stem and branches consist of a tubular ramification, which is in continuity with the lining membrane of the stomachs of the polypes, whilst the external horny integument is continuous with the bell-like polype-cell (Fig. 99). Now it is not here the polype alone, nor the collection of polypes, which constitutes the Zoophyte; for all the polypes may drop-off, like the leaves of a tree, and the polypidom may yet retain its vitality, and may put forth new polypes. Moreover, the new polypes formed by gemmation are not evolved from the pre-existing polypes, but from some part of the stem or branches. The external horny coat softens at a certain spot, and the internal membrane protrudes, pushing (as it were) the horny integument before it (Fig. 230, A); this protrusion increases (B, C), and soon comes to present the form of a polype-cell (D), the mouth of which, however, is still closed. After a time the horny integument thins-away, and at last opens at the projecting extremity, so that the cell assumes its bell-like aspect (E); but the internal membrane does not as yet undergo the same process, so that no polype-mouth is formed. This operation, however, is effected in the next stage (F); and soon afterwards the tentacula are seen, as little wart-like processes around the orifice (G). Up to the time when the mouth is formed, a double current is seen in the stalk of the bud; the particles ascending into it from the stem, passing round its dilated interior, and then descending in its stalk. The whole history of this development, and the connection of the polypes with the nutritive functions alone, show that they must be considered as standing in the same relation to the stock, as the leaves of a tree to its stem and branches; the lining membrane of the polypidom, like the cambium-layer of the tree, being the part in which the developmental capacity chiefly exists. The extension of the

Fig. 230.



Progressive stages of the development of the polype-bud of *Campanularia gelatinosa.*

original stock, after this fashion, may go-on in some species almost indefinitely, the polype-buds, as they are formed, remaining in continuity with the structure of which they are offsets; but there are some zoophytes of this tribe, which are less disposed to ramification, and which, like the Hydra, form detached gemmæ, that henceforth live independently, and develope themselves into new organisms, similar to that from which they were budded-off.

538. In these provisions for the extension of the original fabric, or for the production of new and independent fabrics of the same kind, we have nothing that can be said to represent the true *Generative* process. For *its* performance, however, a peculiar set of buds is developed from the Zoophytic structure, which present a more or less close correspondence to *Medusæ;* these buds, which sometimes remain in connection with the stock, but are frequently detached and swim freely, develope within themselves either ova or spermatozoa; and by the fecundation of the former by the latter, a new generation of embryoes is originated, which are developed into the polype-form, and ultimately produce Medusa-buds in their turn.—One of the simplest and best examples of this process, that serves to connect the *Hydra* (in which no special organ for the evolution either of sperm-cells or of germ-cells is present) with the ordinary *Tubularian* and *Sertularian* Zoophytes (in which free Medusæ are budded-off), is that of *Cordylophora,* the history of whose generative process has recently been admirably elucidated by Prof. Allman.* This Zoophyte, in the later summer and autumn months, evolves a set of ovoid capsules; which at first present themselves (Fig. 231, A) as simple protrusions of the branches on which they grow, each containing a diverticular prolongation of the soft interior substance of the stem; but which, when more fully evolved (B), is seen to contain a sac filled with cells, over which is distributed a network of passages, that branches-off from the diverticulum at its base. Some of these capsules are filled with a turbid fluid, which, when forced-out by pressure, is seen to contain spermatozoa (C, L, M); whilst others exhibit ova in their interior (D), which speedily undergo the process of segmentation. Whilst this is proceeding to the formation of a 'mulberry mass,' the cellular sac with its system of ramified tubes disappears; and the cluster of ova (numbering from two or three to eight or ten) is seen lying upon the diverticulum (E). The ova then begin to elongate themselves and lose their mulberry-like aspect, becoming smooth, and presenting a transparent margin (F); they soon commence moving in the interior of the capsule: and by the rupture of its summit they escape into the surrounding water, through which they swim in the form of infusory animalcules with short cilia (G). At this period, the embryo (H) consists of an outer and an inner layer of cells, with a hollow interior; after some little time the cilia disappear, one extremity becomes expanded into a kind of disk by which it attaches itself to some fixed object; and the mouth begins to be formed (I). The embryo soon increases in length and thickness; tentacula (usually four in number) begin to shoot forth round the mouth; and other changes take place, which approximate it to the single polypes of the parent stock (K). The stem elongates, stolons are sent forth from its base, from which new stems spring-up; and by the formation of lateral gemmæ from the original stock and secondary stems, the

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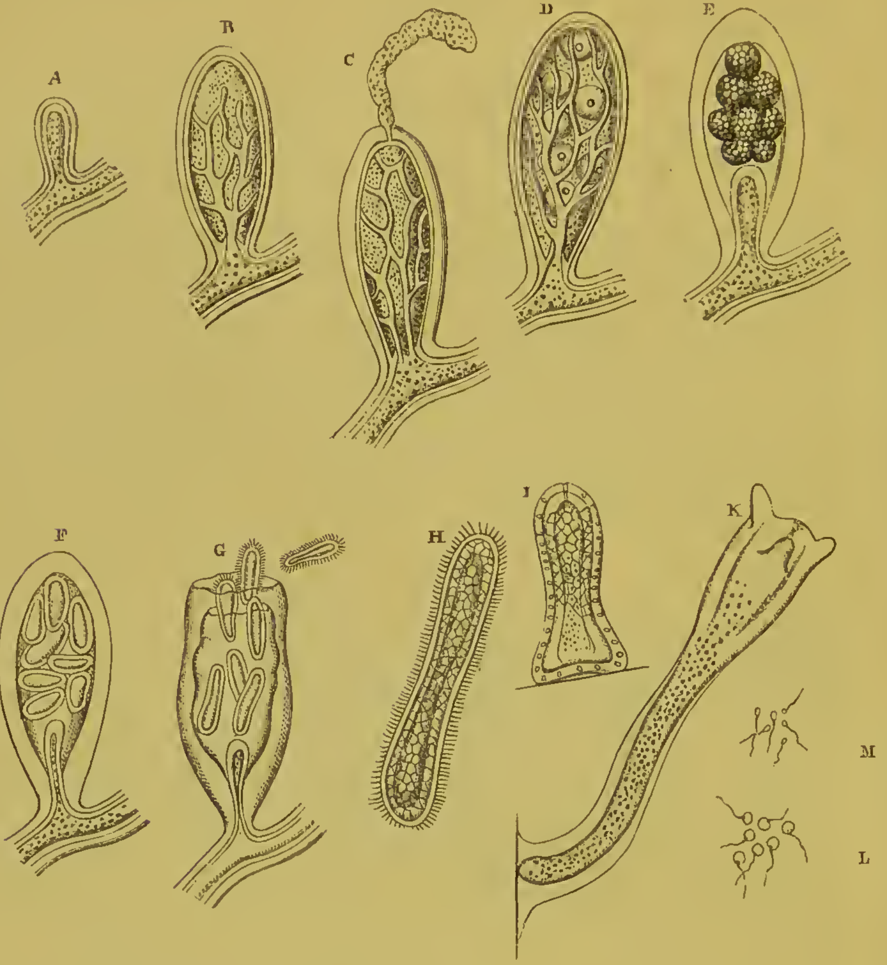
* "Philosophical Transactions," 1853, p. 367.

characteristic fabric of this Zoophyte is progressively evolved.—It is justly remarked by Prof. Allman, that if we compare these capsules with

Fig. 231.

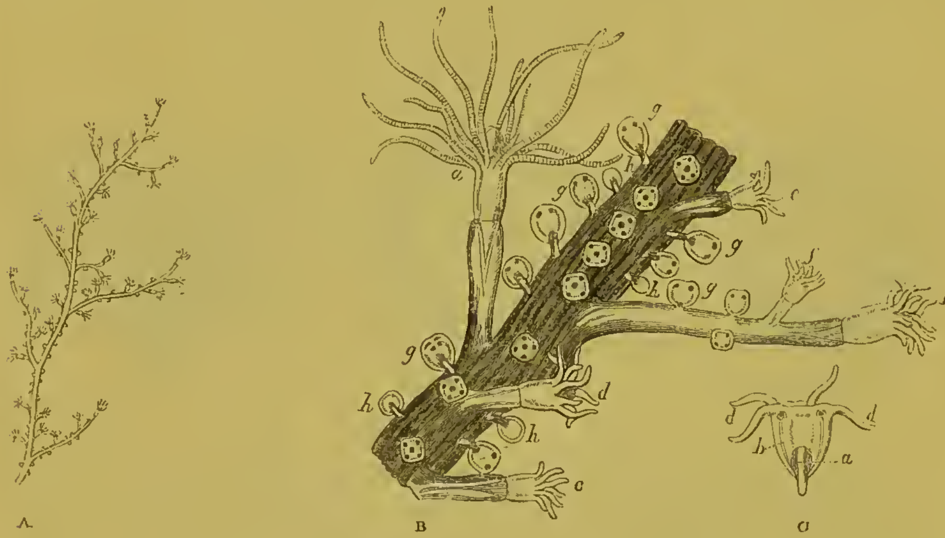


Generation and Development of *Cordylophora lacustris*:—A, ovigerous capsule in early stage; B, the same in more advanced stage, showing cellular sac and ramified canals; C, seminiferous capsule, emitting spermatic fluid; D, ovigerous capsule containing ova; E, the same, with the ova in the mulberry-condition, the ramified canals having disappeared; F, a capsule still further advanced, the ova elongated and smooth, and the diverticulum nearly withdrawn; G, the capsule ruptured, and the embryoes escaping in the condition of free ciliated Infusoria; H, embryo just after its escape, more highly magnified, presenting an internal closed cavity, surrounded by two layers of cellular membrane; I, embryo after the loss of its cilia, pyriform, and attached by one extremity; K, embryo, now assuming the polype-form, the tentacula beginning to bud-forth, and the stem being surrounded by a delicate polypary; L, caudate cells liberated from seminiferous capsule; M, spermatozoa escaped from them.

the true Medusa-buds of other Hydroid Zoophytes, we see that they are only a less-developed form of the same type; the organized cellular sac being homologous with the disk of a Medusa, and the central fleshy column representing the peduncle or proboscidiform stomach, while the system of branched tubes answers to the gastro-vascular canals. Since neither the male nor the female capsule can be observed to open previously to the segmentation of the ova, the act of fecundation would seem to be effected by the passage of the spermatozoa through the cavity of the stem and branches.

539. In other Zoophytes of the families *Tubularidæ* and *Corynidæ*, the capsules have more of the Medusan character; and they detach themselves from the stock from which they are budded-off, before either spermatozoa or ova can be detected in them. Such is the case, for example, with *Perigonimus muscoides*, as described by Sars.* The Medusa-buds, in the first instance, are merely, like the polype-buds, little protuberances (Fig. 232, B, *h h*) developed from the soft tissue of the interior, and attached by a footstalk; they soon, however, present a quadrangular form, and four spots are seen, which are the nuclei or centres of growth whence the marginal cirrhi are afterwards to be developed (*g*, *g*). After a further interval, an aperture forms itself at the most projecting part of the bud, which thenceforth has somewhat the form of a bell (C); and the stomach (*a*) is seen at its deepest portion, with four radiating canals (*b*, *b*) proceeding to its marginal cirrhi. As these buds approach their maturity, they exhibit independent movements, and at last become detached and swim-away freely, being propelled, like the ordinary Medusæ, by the rhythmical contractions of the disk. Their further development proceeds, therefore, altogether independently of the organism by which they were evolved; they capture and digest their own food, and thus nourished they increase in size and probably undergo some changes in form; and true generative organs being subsequently developed in them, fertile ova are formed, as in the ordinary Medusæ, which will doubtless be developed, in their turn, into the Zoophytic structure, whence similar medusa-buds

FIG. 232.



Development of Medusa-buds from *Perigonimus muscoides*;—A, part of a polype-stem of its natural size;—B, portion of the same enlarged, showing *a*, a polype with its tentacula expanded, *b c d e f*, other polypes in various states of contraction, *g g*, medusa-buds showing the four nuclei, *h h*, medusa-buds less advanced;—C, medusa-buds more advanced and detached, showing *a*, the stomach, *b*, the four radiating canals, *d d*, the marginal cirrhi.

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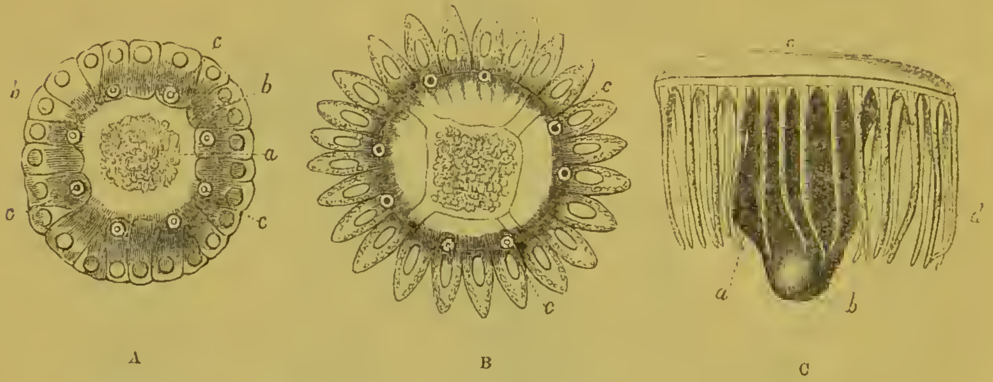
* "Fauna littoralis Norvegiæ," p. 8.

will in due time be put-forth.—In certain forms of both these families, both attached and free generative buds are developed, the former strongly resembling the ovigerous capsules of Cordylophora, whilst the latter correspond with the medusa-buds of Perigonimus; but no difference can be traced in their respective products.*

540. In the *Campanularidæ* and *Sertularidæ*, similar buds are developed within the capsules which have been usually termed 'ovarian' or 'ovigerous' (Fig. 99, *e*); which capsules have been shown by Prof. E. Forbes† to be in reality metamorphosed branches. These medusa-buds spring, not from ova, but from a detached portion of the medullary substance;‡ and they are gradually developed, even while yet contained within the capsule, into the Medusan type (Fig. 233). Here, too, the marginal cirrhi are seen to spring from the nuclei of elongated cells that form the margin of the primitive disk (A, *b*); and the central stomach (*a*) occupies the place which was at first filled by the projection of the medullary substance. As the time approaches for the opening of the capsule, the cirrhi undergo elongation, and the four canals proceeding from the central stomach to the margin (a disposition of parts especially characteristic of the Medusæ) are now seen (B). The buds then become detached from their foot-stalks, and begin to exhibit active movements in the interior of their capsules; and at last an opening is formed in the latter, either by the dehiscence of a lid, or by the thinning-away and rupture of the most prominent portion, through which the young Medusæ swim forth, and disperse themselves actively through the water, their

Fig. 233.



Medusiform gemmæ of *Campanularia gelatinosa* in different stages of development;—A, a gemma not yet escaped from the ovarian capsule, showing *a*, the stomach in progress of formation; *b b*, elongated cells, the rudiments of the cirrhi; *c c*, eye-cells (?);—B, a gemma somewhat more advanced, showing *c c* the eye cells (?);—C, a medusiform gemma freely swimming through the water after its escape; *a*, the body; *b*, mouth; *c*, disk; *d*, cirrhi.

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* See Prof. Van Beneden's admirable "Recherches sur l'Embryogénie des Tubulaires," Bruxelles, 1844.—There can scarcely now be a doubt that in this instance, as in the next, this excellent observer was mistaken in his idea that the Medusoid buds would themselves return to the condition of polypoid stems.

† "Annals of Natural History," 1st Ser., Vol. XIV.

‡ Although they are described by Van Beneden as developed from ova, yet it is clear from his own account that such is not the case; and that what he called the vitellus is continuous with the medullary substance of the stem and branches of the zoophyte. See his beautiful "Mémoire sur les Campanulaires," Bruxelles, 1843.

marginal cirrhi being now developed, and the proboscis and stomach being adapted for the reception and digestion of food (c). Here, as in the preceding case, a deficiency must be confessed, as to our knowledge of the subsequent stages from actual observation; but as this knowledge *has been* completely attained in a case which seems in all essential respects parallel (to be described in the next paragraph), there can be little doubt that, as in the preceding case, the medusa-bud evolves itself into the perfect Medusan type, developes sexual organs, performs the true generative process, and thus produces real ova, from which a zoophytic structure, similar to that which gave-off the medusa-buds, is again evolved.—It has been observed by Lister* and Lovén,† that the medusa-like bodies generated in the interior of the 'ovigerous capsules,' instead of becoming completely detached and freely swimming forth, sometimes expand at the summit, generate and set-free their ova in the condition of ciliated 'gemmules,' and then wither like blossoms, to be succeeded by a new expansion. In other instances again, the medusa-buds do not even expand themselves at the mouth of the 'ovigerous capsule,' but may perform the generative process in its interior, and may thus set free ciliated gemmules without ever themselves existing in the condition of independent Medusæ.‡ In *Sertularidæ*, the generative zooids do not seem ever to possess locomotive powers.—Similar varieties will be shown to exist among the Composite Acalephæ (§ 547).

541. We have thus seen that the animal fabrics which are known to the Naturalist as *Compound Hydroida*, whilst extending and multiplying themselves by ordinary gemmation, perform their true Generative operation through the intermediation of organisms possessing all the essential characters of true *Medusæ;* and that these may either develope and fertilize their ova whilst still in organic connection with the stock, or may detach themselves from it, and maintain their existence as independent zooids. It has now to be shown that the bodies with which the Naturalist is familiar in the condition of true *Medusæ*, really commence life in the polypoid state, and may be regarded as gemmæ budded-off from a *Polype-stock*. The very curious history now to be given, has been ascertained by the united labours of many observers; and the process may be now regarded as having, in all its essential features, been clearly elucidated.§—The generative organs of the *Medusæ*, are contained in four 'ovarial chambers' surrounding the mouth, and opening by orifices of their own (Fig. 36). Within each of these chambers is seen a plaited riband-like membrane, between the folds of which are developed, during the period of fertility, either spermatic cells or ovules. As these usually exist in separate individuals,‖ and as no means can be discovered for the conveyance of the seminal fluid of one to the ovarial chambers of the other, it

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* "Philosophical Transactions," 1834.

† "Wiegmann's Archiv." 1837.

‡ See Allman, loc. cit., p. 379.

§ See especially the Memoirs of Sars in "Isis," 1833, and "Wiegmann's Archiv.," 1837 and 1841, and his "Fauna littoralis Norvegiæ;" Siebold in "Beitrage zur Naturgesch. Wirbellos. Thiere," and in "Froriep's Neue Notizen," 1838; Steenstrup in his "Alternation of Generations," translated and published by the Ray Society; and Sir J. G. Dalyell's "Rare and Remarkable Animals of Scotland," Vol. I., Chap. III.

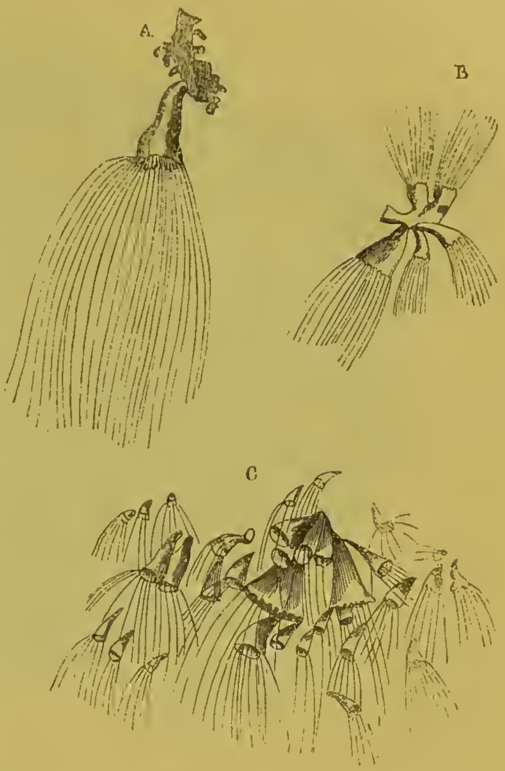
‖ It has recently been asserted by M. Derbès ("Ann. des Sci. Nat.," 3e Ser., Zool., Tom. XIII., p. 377), that the *Cyanæa chrysaora* is hermaphrodite; but it does not appear certain that he has not mistaken the 'thread cells' or urticating organs for sperm-cells.

is probable that fecundation is effected in the same manner as in many Mollusca and Fishes,—the fluid being dispersed through the water in the neighbourhood of the ova, with which they thus come into contact. A very curious provision for the protection of the embryo during its subsequent development, is found in some Medusæ. Small pear-shaped bags or pouches are appended to the fringes of the tentacula; and into these are conveyed (in what mode, however, is unknown) from four to eight germs, which undergo their development within them, and which, when perfected, make their way out by the rupture of the sac. In this curious disposition, we are reminded of the peculiar development of the Marsupial Mammalia.

542. The embryo emerges from the marsupium in the condition of a ciliated gemmule, of a rather oblong flattened form, very closely resembling an Infusory Animalcule. In this grade of development, it has no mouth; but the central cells deliquesce, so as to form a cavity, which is to be the future stomach. The next change consists in the enlargement of one end of the embryo, and the contraction of the other; the latter is developed into a suctorial base or foot, by which the animal attaches itself to some fixed object; whilst in the former a central depression is soon observed, which gradually deepens until it communicates with the internal cavity, thus forming a mouth, and four tubercles that are seen around it are gradually elongated into tentacula, which are afterwards augmented in number.—Thus the first product of the ovum is not a Medusa, but a Hydra-like polype; and the resemblance is not limited to external form, but extends to internal structure, and to the mode of existence and multiplication. For this *Strobila* (as the polypoid larva of the Medusa has been termed), attaching itself by its base to a fixed object, spreads its arms (which are furnished with urticating organs) through the water in search of prey (Fig. 234, A); and by their means its food is drawn into the stomach, whence the indigestible residue is ejected through the mouth, just as in the Hydra. Further, the polype multiplies itself by gemmation; and this not only by the development of lateral gemmæ from its body (B), but also in some instances by the evolution of a *stolon* or creeping stem from its base (resembling that of many Zoophytes), from which gemmæ sprout forth, these generally becoming subsequently detached. Thus from a single individual, a large colony (C) may be produced in no very long time, the detached gemmæ most commonly remaining in proximity with each other; and the rate of multiplication, as in the Hydra, is chiefly influenced by the temperature, and by the supply of food. Further, it has been ascertained by Sir J. G. Dalyell (Op. cit.), that this creature has the same power of regenerating parts of the body that have been removed, or of reproducing the complete body and tentacula from a portion of it, as that which is possessed by the common Hydra; and that both portions of a bisected Strobila could not merely be developed into new and perfect individuals, but could multiply the stock by gemmation, as before their fission. There appears no definite limit to its continuance in this state; it was kept by the last-named excellent observer for several years; and from the entire conformity of its general structure and habits to that of the Hydra, and the absence of any indication of its *larval* nature, it was considered by him as a complete being, 'entitled to a distinct position in the *Systema Naturæ*.'—A

minute examination of its structure, however, shows that it is distinguishable from the ordinary Hydraform polype. The part surrounding the mouth is capable of being protruded as a sort of proboscis; and the aperture of the mouth is then seen to have a quadrangular form. The inner surface of the lips and mouth, and the external surface of the tentacula and body, are covered with cilia; so that currents of water, unless when the mouth is shut, are continually passing in and out from the mouth and along the tentacula. No proper Hydroid polype has its arms or body ciliated. The wall of the stomach consists of two layers, of which the inner one is folded inwards so as to form four longitudinal projections into the cavity of the stomach, a sort of pouch or blind canal being left between the folds of each plait. These four short canals terminate at the upper end in another canal, that passes between the outer margin of the mouth and the periphery of the disk; and into this circular canal, the tubular cavities of the tentacula also open.* This arrangement is obviously indicative of the Medusan affinities of the Strobila; but it does not render it the less a Polype.

Fig. 234.



Strobila (or polypoid state of *Medusa*) propagating by gemmation:—A, single individual, attached by its base, its tentacula extended in search of food; B, a group of five, the gemmæ remaining in connection with the parent; C, a colony, consisting of numerous zooids proceeding from a common stock, but most of them detached from it.

543. The *Strobila* does not always remain, however, in this phase of development. Under certain conditions not yet ascertained, it ceases to multiply by ordinary gemmation, although this process may have gone-on with regularity and activity for months and even years previously; and enters upon an entirely different series of operations, of which the first is the assumption of a more elongated cylindrical form than it had previously possessed. A constriction or indentation is seen around this cylinder, just below the ring which surrounds the mouth and gives origin to the tentacula; and similar constrictions are soon repeated around the lower parts of the cylinder, so as to give to the whole body somewhat the appearance of a *rouleau* of coins (Fig. 235). Still, however, a sort of fleshy bulb, somewhat of the form of the original polype, is left at the base or attached extremity (Fig. 236, A). The number of circles is indefinite; and all are not formed at once, new constrictions appearing

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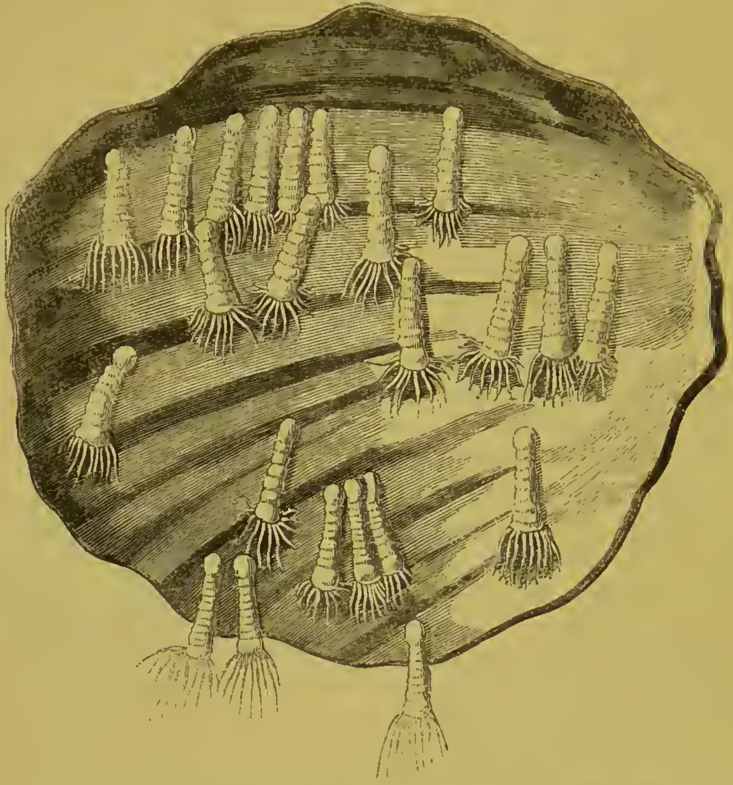
* This description is derived from the excellent 'Observations on the Development of the Medusæ,' by the late Dr. John Reid, contained in the "Annals of Natural History" for Jan. 1848, and in his "Physiological, Pathological, and Anatomical Researches."

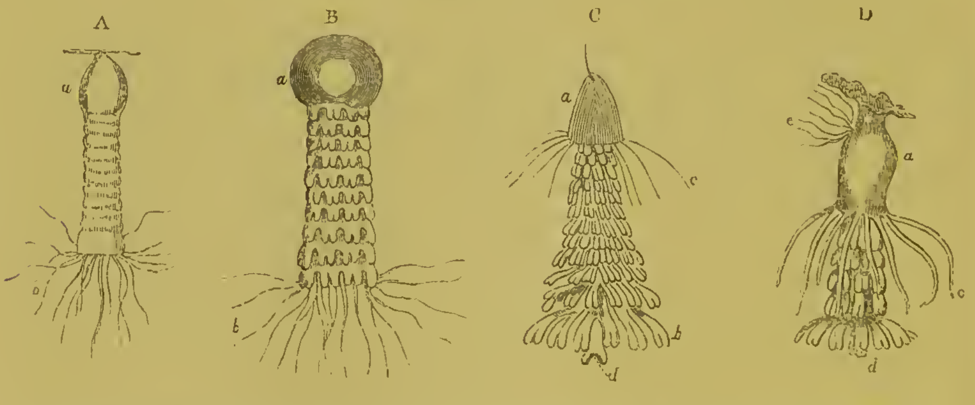
below, after the upper portions have been detached; as many as 30 or even 40 have thus been produced in one specimen. The constrictions then gradually deepen, so as almost to divide the cylinder into a pile of saucer-like bodies; the division being most complete above, and the upper discs

Fig. 235.



Group of *Strobilæ*, or *Medusan Larvæ*, attached to a shell of Pecten.

Fig. 236.

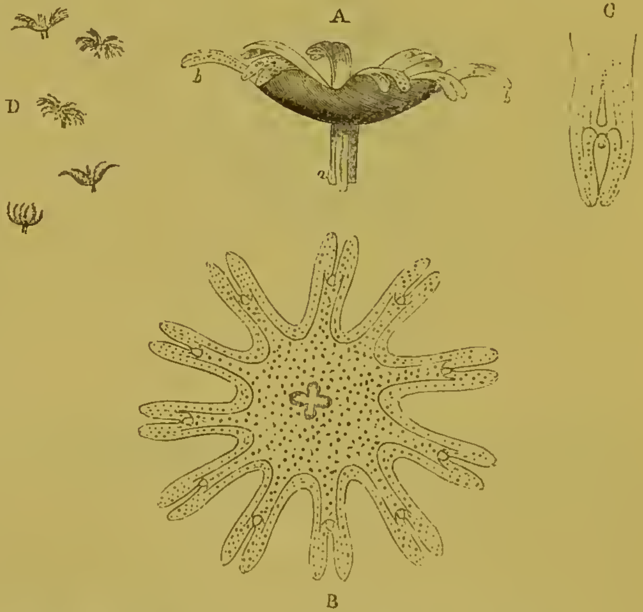


Development of Medusa-buds from Strobila:—A, Strobila enlarged, with incipient production of disc-like gemmæ between the body *a* and the circle of tentacula *b*;—B, more advanced development of the Medusa-buds, the constriction between them being deepened, and their margins becoming lobed;—C, a specimen still further advanced, the original tentacular circle being now detached, and a new set of tentacula *c* developed at the base of the pile of discs, of which those nearest the extremity *b* are most advanced, having acquired the proboscis *d*, and the general form of the Medusa;—D, a Strobila returning to its original polypoid state, several of the Medusa-buds having been detached, the new tentacula *c* being fully developed, and a polype-bud *e* being in process of formation.

usually presenting some increase in their diameter; and whilst this is going-on, the edges of the discs become lobed, and the lobes soon present the clefts and ocelli characteristic of the detached Medusæ (B). Up to this period, the tentacula of the original polype surmount the highest of the discs; and a general contraction and relaxation of the whole cylinder, causing the intervals between the discs to be diminished or increased, may be occasionally seen to take place. But before the detachment of the topmost disc, the circle of tentacula around the original mouth disappears; and a new circle is developed upon the summit of the bulb, which remains at the base of the pile of discs (C). At last, the topmost and largest disc begins to exhibit a sort of convulsive action; it becomes detached, and swims freely away; and the same series of changes takes place from above downwards, until the whole pile of discs is detached and converted into free-swimming Medusæ. But the original polypoid body still remains; and may return to its polype-like and original mode of gemmation (D), becoming the progenitor of a new colony of *Strobilæ*, every one of which may develope in its turn a pile of medusa-discs.*

544. The bodies thus detached have all the essential characters of Medusæ. Each consists of an umbrella-like disc, divided at its edge into a variable number of lobes, *eight* being apparently the normal type; and of a stomach, which occupies a considerable proportion of the disc, and projects downwards in the form of a proboscis, in the centre of which is the quadrangular mouth (Fig. 237, A, B). At first there are no indications of genital organs; but these subsequently appear. Each of the lobes of the margin is bifid; and at the bottom of the cleft is a little body which has been supposed to be a rudimentary eye (C); but it is very doubtful whether it is really entitled to this designation. As the animal advances towards maturity, the segments or lobes of the border of the disc increase comparatively little in size, whilst the intervals between them gradually fill-up; tubular prolongations of the stomach extend themselves over the disc; and its borders become furnished with long, pendent, prehensile cirrhi. The

Fig. 237.



Development of *Medusæ* from detached gemmæ of *Strobila*;—A, individual viewed sideways, and enlarged, showing *a* a proboscis, and *b* bifid lobes; B, individual seen from above, showing the bifid lobes of the margin, and the quadrilateral mouth; C, one of the bifid lobes still more enlarged, showing the ocellus at the bottom of the cleft; D, group of young Medusæ as seen swimming in the water, of the natural size.

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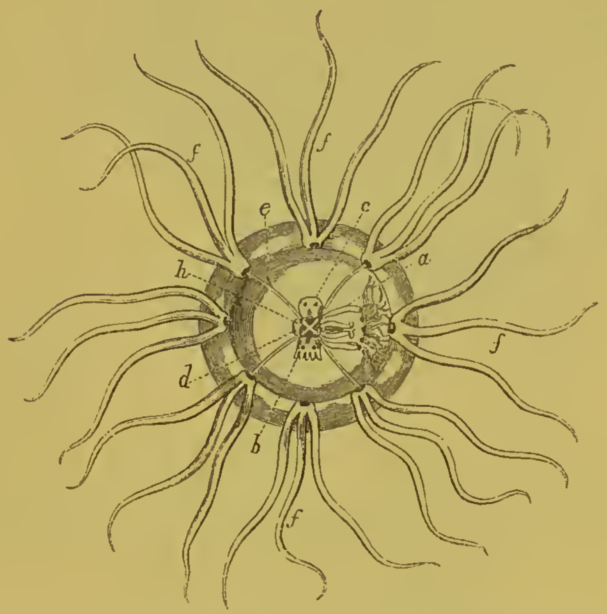
* This last fact, which is of fundamental importance in the philosophical interpretation of this wonderful process, was first brought to light by Sir J. G. Dalyell (Op. cit.)

mouth, which even in the youngest detached animal admits of being greatly extended and protruded, is quadrangular, and presents four extensible angles. These angles grow more rapidly than the four-sided oral tube or proboscis; so that, in the more advanced animals, the mouth appears during the growth to have divided or split into four lobes; and the minute serratures which appear on the edges of these, are the commencement of the lobes and fringes that are observed on the tentacula of the adult animal.—The Medusæ which are as yet known to be developed after this mode, belong to the 'hooded-eyed' group of *Pulmograda;* whilst those which are budded-off from the composite Hydroid Zoophytes belong to the 'naked-eyed' subdivision. Even after the complete Medusan form has been attained, multiplication occasionally takes place by gemmation; but only, so far as yet observed, in the inferior or 'naked-eyed' group. This curious fact was first observed by Sars* in *Cytæis;* from the peduncular stomach of which he observed medusan gemmæ to arise, these being symmetrically arranged around its four sides, but in different stages of advancement (Fig. 238). He also observed in *Thaumatias* a similar gemmation from the ovaries. Both these observations have been verified by Prof. E. Forbes, who has also seen in a species of *Sarsia* an evolution of gemmæ around the whole length of the peduncle, these being in different stages of development, and having an indistinct spiral arrangement; whilst in another *Sarsia* he has found clusters of gemmæ hanging like bunches of grapes from the tubercles at the base of the four marginal cirrhi.†

Fig. 238.



Gemmiparous multiplication of *Cytæis octopunctata*;—*a*, *b*, *c*, *d*, buds in different stages of development, sprouting from the wall of the stomach *h*; at *e* is seen one of the four radiating canals; at *f f f* the marginal cirrhi, and at *h* the proboscis.

545. Now if the history of the generation and development of the Medusæ be compared with that of the corresponding processes in the Hydroid Zoophytes, it will be seen that the two series of phenomena are of precisely the same order. The immediate product of the ovum, in each case, is a Hydraform polype. This lives for an indefinite time in the polypoid condition, and multiplies itself by gemmation; the gemmæ either detaching themselves, so as to form distinct zooids; or remaining in continuity with the original stock. But to whatever extent this

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* "Fauna littoralis Norvegiæ," p. 10.

† "Monograph of the British Naked-Eyed Medusæ," published by the Ray Society, 1848, p. 17.

process is carried-on, it merely consists in a multiplication of the original Hydra; and all the zooids thus produced have the same *homological* relation to each other, as have the several parts of any single body among the higher Animals. But, under some change, either of internal or of external conditions, which cannot yet be distinctly stated, the *polypoid* gemmation gives place to the *medusan*,—the multiplication of the products of the original generative act, to the preparation for a repetition of that act. Now although the Medusa-buds of the *Strobila* are formed in a different situation from those of the *Coryne* or *Campanularia*, being developed between the body and tentacular circle of the original polype in the one case, and from the sides of the polype-body or from the connecting stem in the other, yet there is otherwise no essential difference between the two operations. In the Strobila, as in the Coryne and Campanularia, the original polype-body remains; so that, after having given-off a large number of medusa-buds, it continues its ordinary polypoid-existence, and may repeat the same process at a future time.* It is in the Medusa-buds only, that *generative* organs are evolved; these are subservient, in the one case as in the other, to the performance of the true generative process; and it is from the ova thus produced, that the polypoid larvæ arise.

546. That the whole of this series of processes is the continuation of one and the same developmental operation, and that the Polypoid and Medusan states should be included in the idea of *one generation*, instead of being regarded as *distinct generations*, will further appear from this consideration; that they do, in fact, hold the same relation to each other, both homologically and functionally, as do the nutritive and generative organs in higher animals. The polype is no more a complete organism, than is the larva of an Insect or the tadpole of a Frog; for, although possessed of the capacity to maintain its own life, it has no generative apparatus for the continuance of the species.—So, again, we do not consider a Plant as having attained its complete development, however great may be its extension by leaf-buds, until it has developed flowers and produced fruit. The Medusan 'zooid' is obviously the flower-bud or generative apparatus of the polype; it originates in a process of continuous development, precisely resembling that which evolves the generative organs, both in the annual Plant and in the Animal, *after* the nutritive apparatus has attained nearly its full development; and its special endowments obviously have reference to its peculiar function, that of propagating the race in localities remote from the original stock. In some of the Campanularidæ, as we have seen, the Medusa-buds never become completely detached from the Zoophytic structure, but seem to remain dependent upon it for their nutriment; and here the embryoes seem to have an unusual motor power, which serves for their dispersion.

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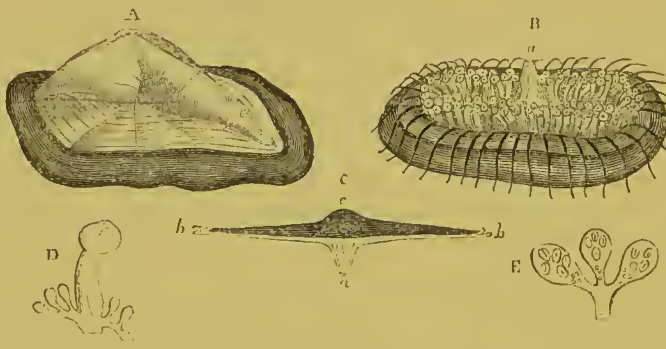
* The production of Medusæ from the *Strobila* was represented by Sars as the result of *fission;* the fact that the polypoid body remains behind, forms a new set of tentacula, and may again give off polypoid and medusan gemmæ, not being known to him. This view is taken-up by Steenstrup, who goes so far as to maintain that the original polypoid animal is really a Medusa of the female sex, which acts as a sort of *nurse* to a brood of young ones. How these young ones are developed, whether from ova or gemmæ, he does not clearly explain; but he considers them as a new generation, *alternating* with the polypoid form,—a mode of viewing the subject which tends to confuse the essential distinction between the product of Gemmation and that of the true Generative act (§ 478).

In most other cases, however, the Medusa-buds are not only detached, but, being separated when as yet they have attained but a small size and a low grade of development, they become provided with a nutrient apparatus of their own, whereby they can obtain and prepare the needful materials. This is perfectly conformable to what has been shown to take place in the Fern (§ 493). Of the detachment of a self-moving body containing the generative products, we shall meet with several curious examples, among the higher Animals.

547. The Generative process among other tribes usually assembled together under the class of *Acalephæ*,* is not less remarkable. In all of them, as it would appear, is there a double method of multiplication, namely, by gemmation, and by true generation; but the results of the former process differ very considerably in the different groups.—In *Beroe* (Fig. 102), as probably in other *Ciliograda*, gemmæ are occasionally produced, which seem to evolve themselves into the likeness of their stock; but the ordinary method of reproduction is by true generation, their progeny being apparently developed at once into the parental form. If this prove to be the case (which is not yet certain), it constitutes an important point of agreement between the Ciliograda and the Helianthoid Zoophytes.—The *Cirrhigrada* may really be considered as composite polypoid animals, analogous to the compound Hydroida, although their parts have a different arrangement, as seen in the *Velella*, Fig. 239.

FIG. 239.



Velella limbosa: A, in its usual position; B, the under surface, showing *a* the central polype-mouth, surrounded by the tubular cirrhi and tentacula; C, side view of the digestive apparatus, showing *a* the mouth, *b b* the bifurcating extremities of the gastric cavity, *c* the liver (?); D, one of the cirrhi, with the medusoid buds attached; E, medusoid buds enlarged.

The multiplication of the nutritive organs (every one of the so-called tubular cirrhi being a distinct polype) takes place by a process of gemmation, the central proboscis-like organ (B, *a*) being the stock, and the surrounding cirrhi the buds; and their cavities all communicate with each other and with the central reservoir, thus forming a polygastric digestive apparatus. The generative act is provided-for by the development of a distinct set of gemmæ around the bases of the cirrhi (D, E); these, which were formerly designated 'ovarian capsules,' are now recognized as medusoid buds; they become detached in some animals of this group, and swim freely through the water; and in due time, they produce either spermatozoa or ova. From each of the latter, when fertilized, a single polypoid animal originates; and this gradually evolves the composite structure by gemmation. The order *Physograda* includes a great number of forms, whose true nature was long misunderstood, but which are now shown to be, like the preceding, composite organisms, the multiplication of whose parts is effected by gemmation. This is the case with the *Physophoridæ* and *Diphydæ*, two groups whose relation to the Medusæ seems to consist in this,—that the contractile natatorial organ, which is developed in the latter around the stomach, is developed separately and on one side of it in the former. In each of these, long chains may be formed by the multiplication of similar organs by gemmation; but there is always a separate provision for the generative process, consisting of a gemma of a peculiar kind, which contains within it either ovisacs or sperm-cells. Both sets of these are formed in each individual of the Physophoridæ, as in monœcious plants; but only one set in each individual of the Diphydæ, as in diœcious plants. This gemma, in some instances, is not developed into any special form, but is a mere protuberance containing the essential organs within it; in other cases, however, it has a natatorial disc developed around it; and some of those which are provided with this organ become detached, and swim about after the manner of Medusæ.—The *Physalia* is simply one of the Physograda, in which the air-vesicle that all possess has undergone an unusual development; and its cirrhi are so many polype-mouths, or portions of a polygastric digestive apparatus. Its reproduction is effected after the same manner; the ova being developed within a medusiform gemma, that possesses a power of independent movement, and the spermatozoa within a gemma of less specialized character; whilst, from the ova which are thus generated and fertilized, a polypoid animal would probably spring, which would gradually evolve itself by gemmation into the likeness of its parent.

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* See the Authors referred-to in the note to § 142.

548. In the class *Echinodermata*, in which the Radiated type is carried to its highest degree of development, the structure of each organism being more complex, and its parts more specialized and mutually dependent, the power of reproduction in any other mode than by sexual generation seems to be almost entirely wanting, notwithstanding that they retain a very extraordinary power of regenerating lost parts (§ 473).* The *Synapta*, one of those aberrant forms of the family Holothuriada which lead towards the Articulated series, presents the only example of spontaneous fission that is known to occur in this class; and of multiplication by gemmation there is probably no instance. In this genus there is another departure from the usual type; the two sets of sexual organs being combined in the same organism, instead of being separated, as in all other Echinodermata. The principal varieties in the position of these organs have been already noticed, in the general sketch of the class (§ 40); but it must be remarked that the so-called 'ovaries' are as frequently 'testes' or spermatic organs; the male and female generative apparatus being scarcely distinguishable from one another in this group, either by

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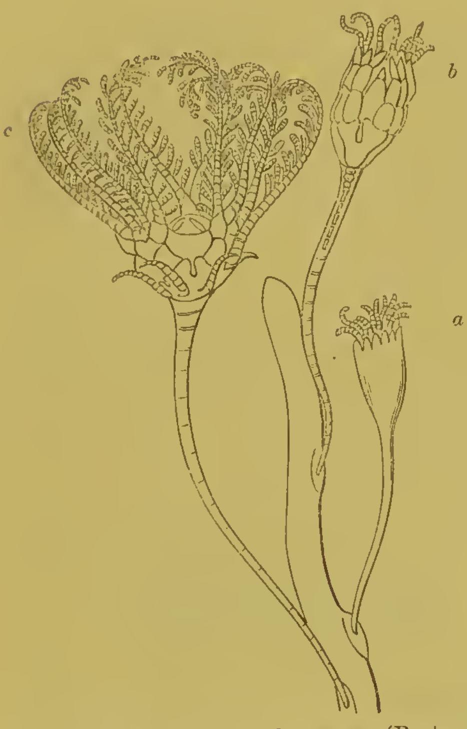
* The Author once met with *a single ray* of a Star-fish in a state of activity, as was evidenced by the energetic movements of its tubular suckers; although it was obvious, from the appearance of the wound, that it must have been detached from the body for some days or even weeks. Might this have continued to live, and have re-formed the body?

their external aspect or their internal structure, except when their respective products are nearly mature. Nothing like sexual congress is known to take place among these animals; so that the ova deposited by the females must be fertilized by the spermatozoa diffused through the sea-water which bathes them.—We have now to trace the history of embryonic development in the Echinodermata, which we shall find to present some very remarkable features.

549. The course of Development of the *Crinoidea* has not yet been followed from its earliest period; and the most important fact which has been substantiated in their history, is the metamorphosis of the pedunculated *Pentacrinus* (Fig. 240) into the free-swimming *Comatula* (Fig. 38), first observed by Mr. J. V. Thompson.* The youngest specimens observed (*a*) had neither jointed column nor arms, but appeared like little clubs fixed by a spreading base, and sending-out from their summits a few pellucid tentacula. The consolidation of the membranous column by the interposition of a calcareous skeleton at intervals, gives to it the jointed character which it subsequently acquires; the arms when first developed (*b*) are simple, their lateral pinnæ (*c*) not appearing until near the period of the change; and the dorsal cirrhi, in like manner, are only evolved as this approaches. In what way, or at what point the detachment occurs, cannot yet be specified; but it seems probable, from the analogies to be presently adduced, that the separation takes place at the summit of the stem.

Fig. 240.



Crinoid state of *Comatula rosacea* (Pentacrinus Europæus); *a*, *b*, *c*, successive stages of development.

550. The most remarkable feature in the development of the Echinodermata generally, is the conversion of the embryonic mass of cells, not into a larva which subsequently attains the adult-form by a process of metamorphosis, but into a 'peculiar Zooid,' which seems to exist for no other purpose than to give origin to the proper Echinoderm by a sort of internal gemmation, as well as (in many cases) to carry it to a distance by its active locomotive powers, thus serving for the dispersion of the species around the spots which would otherwise become overcrowded by the accumulation of individuals. The relative development of this 'Larva-zooid,' and of the 'Echinoderm-zooid,' however, vary considerably in different species. In the first case of the kind observed by Sars,† that of the *Echinaster rubens*, the 'larva-zooid' bears so small a proportion to the 'Asterid-zooid' which it bears, that its independent character

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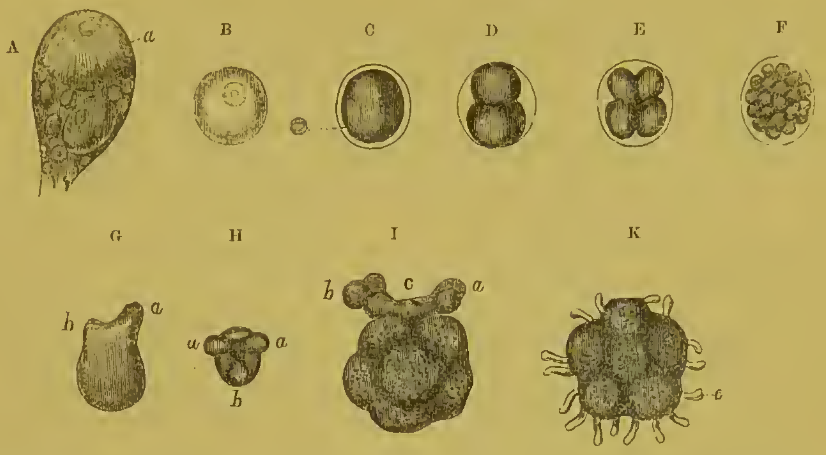
* "Zoological Researches," Part I., and "Edinb. New Phil. Journ." 1836.

† "Fauna littoralis Norvegiæ," 1846; and "Ann. des Sci. Nat.," 3e Sér., Zool., Tom. II., p. 190.

was not observed, until pointed out by Busch[*] and Müller;[†] it having been at first considered as a mere pedicle or organ of attachment, put forth from the embryo-Echinoderm. The evolution of the mulberry-mass by the segmentation of the yolk, takes place as in other animals (Fig. 241, C, D, E, F); and the embryo comes-forth from the egg soon after it has attained this state, and swims freely about, by means of the cilia with which it is covered, in a sort of marsupial chamber which is formed by the drawing-together of the rays of the parent around its mouth. Soon after its emersion, the embryonic mass begins to manifest a separation into two parts, one of which is at once evolved into the 'larva-zooid,' which possesses a stomach and probably a mouth of its own, while the other is subsequently developed into the Asteroid form. The 'larva-zooid' at first possesses two tubercles, the subdivision of one of which soon forms a third (G, H), while a fourth is afterwards formed by the subdivision of the other (I), an apparent mouth being situated in a papillary projection (*c*) between them. At the same time, the principal mass gradually becomes flattened, and shapes itself into five lobes surrounding a central disc; thus sketching-out the body and rays. When in this state, it attaches itself to fixed objects by its organ of adhesion; but if detached, it swims through the water by the action of the cilia with which the surface is clothed. At the same time, five double rows of small tubercles may be perceived, radiating from the centre of what is to become the ventral surface of the body; these gradually elongate themselves, and become cirrhi (K, *e*), each fur-

FIG. 241.



Development of Embryo of *Echinaster rubens*;—A, ovarian cæcum, containing ova in various stages of development, the most mature being seen at *a*; B, ovarian ovum highly magnified, showing the germinal vesicle and spot; C, an ovum after its deposition, the natural size being also shown; D, E, F, successive stages of the segmentation of the yolk; G, embryo soon after its escape from the ovum, showing at *a*, *b*, two of the rudimentary organs of attachment; H, end view of the same, showing all three (*a*, *a*, *b*) of these organs; I, more advanced embryo, attached by four organs, two at *a*, and two at *b*, with a papillary projection *c* between them; K, embryo more advanced, free and furnished with cirrhi, *e*.

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[*] "Beobachtungen über Anatomie und Entwickelung einiger Wirbellosen Seethiere," 1851.

[†] "Uber den allgemeinen Plan in der Entwickelung der Echinodermen," 1853.

nished with a sucker at its extremity. A peculiar tubercle is also seen at the edge of each of the five lobes of the body; and this is the rudiment of the *ocellus*, which is afterwards found at the extremity of each ray. As development proceeds, the 'larva-zooid' which forms the so-called *pedicle*, gradually decreases in size, and the 'Asterid-zooid' creeps by means of its cirrhi; and at last the 'pedicle' is drawn (as it were) into the body, the lobes of the body lengthen into rays, the animal loses its ciliograde progression, and the ordinary characters of the Star-fish become apparent.—The progress of the internal organization is thus described by Agassiz.* The earliest deposit of calcareous matter takes place around the prominent tubercles of the lower surface; at first in the condition of little isolated crystals, which are formed as nuclei in the cells; and then as a network formed by the coalescence of several of these. Of these networks there are at first ten, symmetrically disposed on the ventral surface, in a manner corresponding to the arrangement of the solid plates in Crinoids; but they gradually increase in number, and more distinctly mark-out the rays; new ones being interposed in pairs between those already existing, and small spines projecting from the older ones. The calcareous deposit in the dorsal surface, on the other hand, seems to proceed from a central nucleus above the yolk-mass. The progress of development is obviously from without inwards; the cells on the surface of the yolk-mass being the first to undergo metamorphosis into the permanent structure. Those occupying the central part of the body and 'pedicle' (or larva-zooid), undergo liquefaction; and a kind of circulation is seen in the latter. Gradually what remains of the yolk-mass is more distinctly circumscribed in the interior of the animal, and forms a central cavity with prolongations extending into the rays; but it is not until the 'pedicle' has contracted itself into a mere vesicle, that the mouth of the Asteroid is formed, by the thinning-away of the envelope of the yolk-mass on the lower surface, a little to one side of the base of the 'pedicle;' and it is not until after the formation of the mouth, that the nervous ring can be traced, with its prolongations extending to the ocelli at the extremities of the rays.—The whole course of development on this type is comparatively rapid; and the direct conversion of the greater part of the vitelline mass into the permanent form, seems here to render unnecessary that evolution of organs peculiar to the larva-zooid, which occurs in most other instances.

551. The larvæ of Echinodermata generally are formed upon the bi-lateral type, and have a ciliated fringe on each side of the body, the two being united by a superior and an inferior transverse band, between which the mouth of the Zooid is always situated; and they all have a stomach and intestine, with a separate anal orifice. Their external forms, however, vary in a most remarkable degree, owing to the unequal development of their different parts. The relation of the Echinoderm-zooids to the Larva-zooids also varies considerably. In no instance are the mouth and œsophagus of the latter preserved in the former; a new mouth being always formed in the Echinoderm-zooid, often in a place very different from that of the larva. In the Holothuriada, no other organs of the Larva-zooid are lost in the Echinoderm-zooid, save the mouth and

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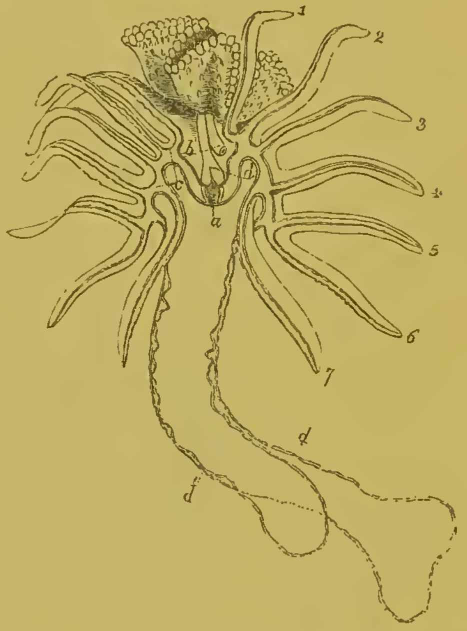
* "Lectures on Comparative Embryology," New York, 1849.

œsophagus, and the ciliated bands; so that the passage from one form to the other more resembles an ordinary metamorphosis. But among the Echinida, Ophiurida, and Asteriada, we generally find that the only part retained is a portion of the stomach and intestine, which is pinched-off (so to speak) from that of the larva. In these three groups, the Echinoderm-zooid developes itself in close apposition with the wall of the stomach, taking its origin in a very minute rudiment, and gradually evolving its characteristic form. The parietes of the body are first distinguished, and the 'water-vascular system' (which is so intimately connected with them) next makes its appearance in the manner already noticed (§ 297, *note*).

552. One of the most remarkable forms of Echinoderm-larvæ is that which has received the name of *Bipinnaria* (Fig. 242), from the symmetrical arrangement of its natatory organs. The mouth (*a*), which opens in the middle of a transverse furrow, leads through an œsophagus *b′* to a large stomach, around which the body of the Asteroid has developed itself; and on one side of this mouth is observed the intestinal tube and anus (*b*). On either side of the anterior portion of the body, are six, or more, narrow fin-like appendages, which are fringed with cilia; and the posterior part of the body is prolonged into a sort of pedicle, bilobed towards its extremity, which also is covered with cilia. The organisation of this larva seems completed, and its movements through the water are very active, before the mass at its anterior extremity presents anything of the aspect of the Star-fish; in this respect corresponding with the movements of the 'pluteus' of the Echinida. The temporary mouth of the larva does not remain as the permanent mouth of the Star-fish; for the œsophagus of the latter enters on what is to become the dorsal side of its body; and the true mouth is subsequently formed by the thinning-away of the integument on its ventral surface. The young Star-fish is separated from the bipinnarian larva, by the forcible contractions of the connecting pedicle, as soon as the calcareous consolidation of its integument has taken place, and its true mouth has been formed, but long before it has attained the adult condition; and as its ulterior development has not hitherto been observed in any instance, it is not yet known what are the species in which this mode of evolution prevails. The larva continues active for several days after its detachment; and it is possible, though perhaps

Fig. 242.

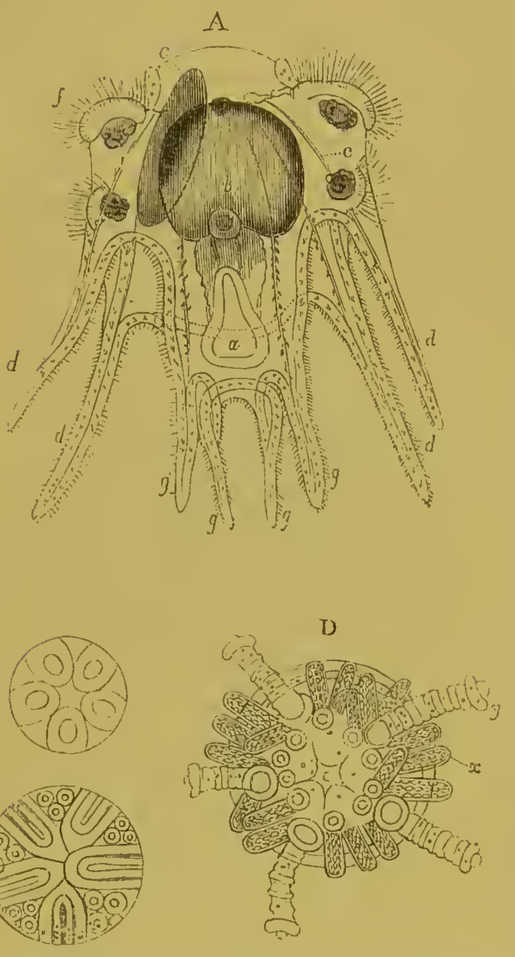


Bipinnaria asterigera, or Larva of Star-fish; *a*, mouth; *a′*, œsophagus; *b*, intestinal tube and anal orifice; *c*, furrow in which the mouth is situated; *d d′*, bilobed peduncle; 1, 2, 3, 4, 5, 6, 7, ciliated arms.

scarcely probable, that it may develope another Asteroid by a repetition of this process of gemmation.*

553. In the Bipinnaria, as in other larva-zooids of the Asteriada, there is no internal calcareous framework; such a framework, however, is found in the larvæ of the Echinida and Ophiurida, of which the form delineated in Fig. 243 is an example.† The embryo issues from the ovum as soon as it has attained, by the repeated segmentation of the yolk, the condition of the 'mulberry-mass;' and the superficial cells of this are covered with cilia, by whose agency it swims freely through the water. So rapid are the early processes of development, that no more than from twelve to twenty-four hours intervene between fecundation and the emersion of the embryo; the division into two, four, or even eight segments taking place within three hours after impregnation. Within a few hours after its emersion, the embryo changes from the spherical into a sub-pyramidal form with a flattened base; and in the centre of this base is a depression, which gradually deepens, so as to form a mouth that communicates with a cavity in the interior of the body, which is surrounded by a portion of the yolk-mass that has returned to the liquid granular state. Subsequently a short intestinal tube is found, with an anal orifice, opening on one side of the body, as was first

FIG. 243.



Embryonic development of *Echinus*;—A, *Pluteus-larva* at the time of the first appearance of the disc; *a*, mouth in the midst of the four-pronged proboscis; *b*, stomach; *c*, echinoid disc; *d*, *d*, *d*, *d*, four arms of the pluteus-body; *e*, calcareous framework; *f*, ciliated lobes; *g*, *g*, *g*, *g*, ciliated processes of the proboscis:—B, disc, with the first indication of the cirrhi:—C, disc, with the origin of the spines between the cirrhi:—D, more advanced disc, with the cirrhi and spines projecting considerably from the surface. (N.B. In figs. B, C, and D, the pluteus is not represented, its parts having undergone no change, save in becoming relatively smaller.)

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* See the Observations of Koren and Daniellsen (of Bergen) in the "Zoologiske Bidrag," Bergen, 1847 (translated in the "Ann. des Sci. Nat.," 3e Sér., Zool., Tom. VII., p. 347); and the Memoir of Prof. Müller 'Uber die Larven und die Metamorphose der Echinodermen,' in "Abhaldlungen der Königlichen Akademie der Wissenschaften zu Berlin," 1848.

† See Prof. Müller, 'Ueber die Larven und die Metamorphose der Ophiuren und Seeigel,' in "Abhaldlungen der Königlichen Akademie der Wissenschaften zu Berlin," 1846. See also, for the earlier stages, a Memoir by M. Derbès, in "Ann. des Sci. Nat.," 3e Sér., Zool., Tom. VIII., p. 80; and for the later, Krohn's "Beitrag zur Entwickelungs-

observed by Krohn. The pyramid is at first triangular, but it afterwards becomes quadrangular; and the angles are greatly prolonged round the mouth (or base), whilst the apex of the pyramid is sometimes much extended in the opposite direction, but is sometimes rounded-off into a kind of dome (Fig. 243, A). All parts of this curious body, and especially its most projecting portions, are strengthened by a frame-work of thread-like calcareous rods (*e*). In this condition, the embryo swims freely through the water, being propelled by the action of cilia, which clothe the four angles of the pyramid and its projecting arms, and which are sometimes thickly set upon two or four projecting lobes (*f*); and it has received the designation of *Pluteus*. The 'pluteus' of the *Ophiura* and that of the *Echinus* at first differ very little in their general form and structure; but the 'plutei' of different species vary considerably in the number of their arms, some having as many as thirteen. The mouth is usually surrounded by a sort of proboscis, the angles of which are prolonged into four slender processes (*g*, *g*, *g*, *g*), shorter than the four outer legs, but furnished with a similar calcareous frame-work. In this condition, the 'pluteus' may be said to present the Acalephoid type, corresponding with the Medusæ in its proboscidiform mouth, and resembling the Beroe in its propulsion by bands of cilia.

554. The first indication of the production of the young Echinus from its 'pluteus,' is given by the formation of a circular disc (Fig. 243, A, *e*), on one side of the central stomach (*b*); and this disc soon presents five prominent tubercles (B), which subsequently become elongated into tubular cirrhi. The disc gradually extends itself over the stomach, and between its cirrhi the rudiments of spines are seen to protrude (C); these, with the cirrhi, increase in length, so as to project against the envelope of the 'pluteus,' and to push themselves through it; whilst, at the same time, the original angular appendages of the 'pluteus' diminish in size, the ciliary movement becomes less active, being superseded by the action of the cirrhi and spines, and the mouth of the 'pluteus' closes-up. By the time that the disc has grown over half of the gastric sphere, very little of the 'pluteus' remains, except some of the slender calcareous rods; and the number of tentacula and spines rapidly increases. The calcareous frame-work of the shell at first consists, like that of the Star-fishes, of a series of isolated networks developed between the cirrhi; and upon these rest the first-formed spines (D). But they gradually become more consolidated, and extend themselves over the granular mass, so as to form the series of plates. The mouth of the Echinus (which is altogether distinct from that of the 'pluteus') is formed at that side of the granular mass, over which the shell is last extended; and the first indication of it consists in the appearance of five calcareous accretions, which are the summits of the five portions of the frame-work of jaws and teeth that surround it. All traces of the original 'pluteus' are now lost; and the larva, which now presents the general aspect of an Echinoid animal, gradually augments in size, multiplies the number of its plates, cirrhi, and spines, evolves itself into its particular generic and specific type, and undergoes various changes of internal structure, tending to the develop-

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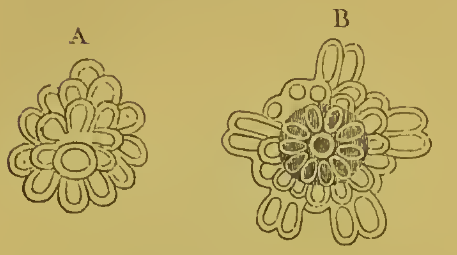
geschichte der Seeigillarven," Heidelberg, 1849, and his Memoir in "Muller's Archiv," 1851.—Prof. Müller has accepted the corrections made by M. Krohn of his own earlier inferences.

ment of the complete organism.—The body of the *Ophiura* takes its origin in a set of little cæca (Fig. 244), which extend themselves from the central mass nearly in the position of the disc of the Echinus; and these grow into a sort of circular cluster (A), which gradually shapes itself into the form of the body of the Ophiura with incipient arms (B). The other changes take place very much after the same fashion as in the Echinus.

FIG. 244.



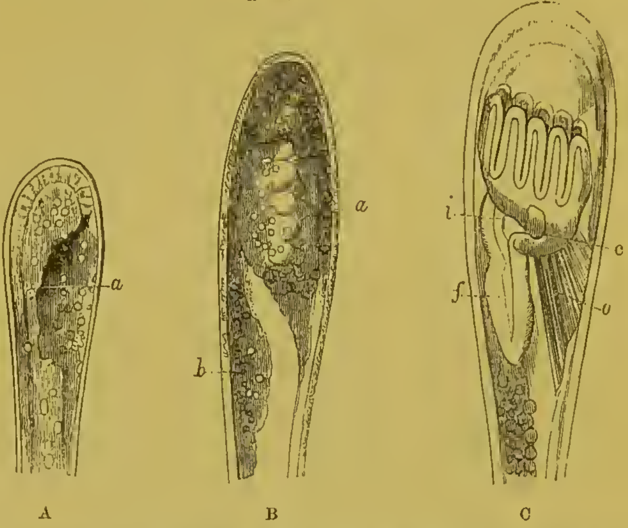
Origin of the *Ophiura* from the side of the stomach in the body of its *Pluteus*:—A, a cluster of cæca; B, the form of the body marked-out, with the commencement of the arms.

555. The developmental processes of which a sketch has now been given, undoubtedly constitute a most remarkable series. We here find the yolk-mass converted into a structure, which is destined only to possess a transient existence, and which disappears entirely by the time that the development of the offset from it has advanced so far, that it begins to assume the characters of the permanent organism. This, however, is what takes place in the higher Vertebrata; for the structures first developed in the egg of the bird hold nearly the same relation to the rudimentary Chick, that the 'Pluteus' bears to the incipient Echinus or Ophiura, or the 'Bipinnaria' to the incipient Star-fish. The only essential difference consists in this, that the development of these temporary structures proceeds so much further in the latter case, as to give them more the character of distinct 'individuals;' and they are endowed with self-moving powers, whereby they are dispersed through the water in this stage of their existence, so as to prevent that accumulation in particular localities, which would otherwise result from the comparatively sluggish habits of these animals in their adult condition. We may trace the analogy yet further; for the 'blastodermic vesicle,' which is cast-off (like the Bipinnaria of the Star-fish) from the fœtus of the Mammal, is gradually taken (like the 'pluteus' of the Echinus) into the body of the Bird; and we have the representation of the type of development first described (§ 550), in the mode of evolution of the Batrachian Reptiles, the whole of whose vitelline mass goes at once to be converted into the embryo, as that of the Echinaster is appropriated by the Asterid-zooid.

556. Passing-on now to the *Molluscous* sub-kingdom, we find in the *Bryozoa* such a close approximation to the Zoophytic type, as regards their multiplication by continuous gemmation, that it is not surprising that their place in the animal series should have been at first mistaken; more especially when the notion prevailed, that no true Mollusk ever multiplies itself by this method. So characteristic is this process, indeed, of Bryozoa, that there is no instance known of an animal of this group existing permanently in a solitary condition, like the Hydra or Actinia; since every Bryozoon, on emerging from the egg, tends to evolve itself into a composite structure, the gemmation taking-place either from the interior of the tubular stem and branches, which usually connect together the cavities of the several cells, or from the cells themselves, where no stem intervenes. The general plan on which this gemmation commences, is

the same as in the Hydraform Zoophytes; for there is first seen a bud-like protuberance of the horny external integument, into which the medullary lining prolongs itself; the cavity thus formed, however, is not to become, as in the group just referred-to, the stomach of the new zooid; but it constitutes the chamber surrounding the stomach, which remains completely enclosed, by the continuity of the membrane lining the cell with that of the visceral sac. The digestive apparatus takes its origin in a thickening of the medullary membrane (Fig. 245, A, *a*), which projects from one side of the cavity into its interior; and the cells of the central part of this appear to deliquesce and form the digestive cavity, whilst from those which surround it are developed the walls of the alimentary canal, the tentacula, and the muscles which protrude or retract this apparatus. The first appearance of the tentacula is seen at B, *a*; and a more advanced stage in the development, the cell being still closed, is shown at C. Whilst these organs are being evolved, the foundation is laid for the generative apparatus, in a similar thickening of the medullary membrane in the lower part of the cell (B, *b*); and this in due time acquires its full development, and matures its spermatic cells.—The Generative organs of the two sexes are usually, if not invariably, united in the same zooids; and are attached to the lining-membrane of the visceral cavity, the testes (Fig. 49, *m*) being situated beneath the stomach, and the ovarium (*n*) near the mouth of the cell.* Both discharge their products by the rupture of their envelopes, into the visceral cavity; and the ova (*o*) lying in this, are fertilized by the spermatozoa which they there meet-with. The manner in which they are finally discharged is not yet ascertained; in *Laguncula*, according to Prof. Van Beneden, they escape by an outlet (*p*) beneath the tentacular circle; but no such outlet has been detected by Prof. Allman in the fresh-water species. The ova are sometimes furnished, before their escape, with a very firm horny casing (occasionally provided with hooked spines), which appears destined to secure them from the effects of the winter's cold, to which the fresh-

FIG. 245.



Gemmiparous extension of *Laguncula repens*:—A, a bud in an early stage of development, showing at *a* a thickening of the interior membrane, which is the first rudiment of the digestive apparatus;—B, the same more advanced, the rudimentary tentacula being now in process of formation, and another thickening showing itself at *b*, as the rudiment of the male generative organ;—C, the same, shortly before the opening of the cell; *c*, buccal cavity; *f*, stomach; *i*, intestine; *o*, retractor muscles.

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* It is asserted by Prof. Van Beneden that the sexes are distinct in some of the fresh-water species; but this is contradicted by Prof. Allman, whose Memoir 'On Freshwater Polyzoa,' in the "Report of the British Association" for 1850, may be referred-to as containing the fullest information on the reproductive processes in that group.

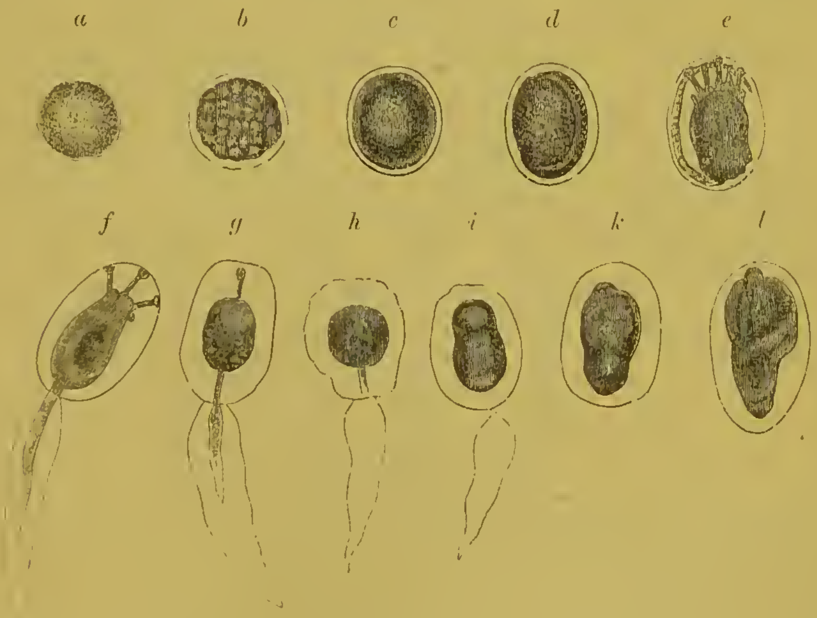
water Bryozoa are more severely exposed than the marine,—being, for the most part, inhabitants of small collections of water, that are liable to be completely frozen. In most cases, however, the embryo is set-free in the state of a ciliated gemmule, from which the first cell, with its highly organized tenant, is gradually evolved; but of the details of its history little is known.

557. The *Tunicata* correspond closely with the Bryozoa in their multiplication by gemmation; for this is the mode wherein all those clusters are formed, which constitute a large proportion of the entire series of these animals; the solitary species, which do not propagate by this method, being almost as exceptional as they are among Zoophytes. In all that group which corresponds in its general structure with the *Ascidian* type, the gemmation takes place externally; and it usually proceeds from a sort of tubular stolon, which extends itself from the base of each zooid (Fig. 138), and which is in connection with the circulating apparatus, so that a double current of blood moves in it. The development of the Ascidian zooid within the buds which arise from this stolon, seems to take place after a mode essentially the same with that of the Bryozoan; but when it has proceeded to an extent that renders the zooid independent of the parent, the circulation through the connecting peduncle usually ceases, so that henceforth the zooid is organically detached from the parent-stock, although remaining included with it in the common envelope. Thus we see that the presence of a general circulation in the clusters of *Perophora* (§ 235), is in reality to be regarded as the persistence of an embryonic character originally common to all the Compound Ascidians. In some of these animals, however, as in many Bryozoa, the gemmation of the zooids takes place directly from the exterior of the body, instead of from a prolongation of it into a stolon.—In the *Salpidæ*, the production of zooids by gemmation takes place after a very different fashion; for the stolon from which they are put-forth is here *internal;* and large numbers of buds are developed from it at the same time. The process commences at a very early period in the life of the 'stock;' for the stolon is distinctly visible before its own embryonic development is completed; and the evolution of the first set of buds commences forthwith, so that it takes place coincidently with the growth of the 'stock' itself. A second group of buds is usually put-forth, and even the formation of a third has often commenced, before the first is ready to be detached. All the buds of each group are detached at the same time; they adhere together by their external surfaces, or by special organs of attachment; and they thus form those chains or clusters of 'aggregate' Salpæ, which are frequently found floating on the ocean-surface in the warmer regions of the globe. Thus whilst the several zooids of the Compound-Ascidian-masses owe their existence the one to the other, and the whole to the primordial 'stock' which laid the foundation of the cluster (thus strictly resembling the relation of the several leaf-buds of a tree to each other and to the original plumule), the zooids forming the Salpa-chains are related only by their common origin from the same stolon, and the 'stock' forms no part of the chain, but remains as a solitary individual.—According to MM. Löwig and Kölliker, a sort of fissiparous multiplication takes place in some of the *Botryllidæ*, at a very early period of embryonic development; each ovum producing, by its segmental division, not a single individual,

but a stellate cluster (Fig. 51). Should such be the case, the phenomenon would be the parallel, in the Animal kingdom, to the free gemmation of Mosses whilst yet in the confervoid state (§ 492). The fact, however, is denied by Prof. Milne-Edwards, who considers that the cluster is formed by subsequent gemmation from the first individual; and the matter remains open for further investigation.

558. Every Tunicated animal of the *Ascidian* type, whether solitary or composite, possesses two sets of sexual organs; an ovarian mass, usually of considerable size, which lies deep in the cavity of the body (Fig. 121, *q*), and is furnished with an oviduct that opens into the cloaca; and a testis (*q*), which usually lies beneath the ovary, and is furnished with an efferent canal (*r*, *r′*) that opens in close proximity with the outlet of the oviduct; so that the ova are fertilized within the cloaca, immediately after their escape from the oviduct, and the changes in which the earlier stages of embryonic development consist, may be usually seen to have taken place previously to the final exit of the ovum from the body. In all the members of this group in which the history of the process has been yet observed, the embryo comes-forth from the egg in a form quite different from that which it is subsequently to present; and is endowed with the power of free locomotion, so important for the dispersion of animals that are to pass the whole remainder of their lives in a fixed condition. The following is a sketch of the history of the process, as observed by Prof. Milne-Edwards in *Amaroucium proliferum*. The yolk appears to undergo the usual segmentation within a very short period after fecundation, so that the 'mulberry mass' (Fig. 246, *b*) is soon produced; and at the same time there is formed between the yolk and the external

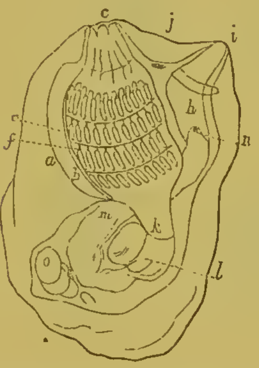
FIG. 246.



Development of the embryo of *Amaroucium proliferum*;—*a*, mature ovum, escaped from the ovary; *b*, ovum taken from the cloaca, advanced to the state of 'mulberry mass;' *c*, *d*, more advanced states of the ovum, still within the cloaca; *e*, ovum whose embryo is ready to emerge; *f*, larva newly escaped; *g*, larva some hours after fixation; *h*, the same, ten hours after fixation; *i*, the same twenty hours after fixation; *k*, the same, at the commencement, and *l*, at the conclusion, of the second day after fixation.

membrane of the ovum, a gelatinous, transparent, nearly colourless layer, which apparently becomes the external tunic or 'test' of the young animal. The marginal portion of the yolk then begins to separate from the central mass, so as at first to appear like a sort of ring encircling it (*c*); but it is soon observable that the apparent ring is really a tapering prolongation, which encircles the central part of the yolk, adhering by its base, and having its extremity free (*d*). A further change takes place, previously to the exclusion of the egg; for the tail-like appendage becomes more and more separated from the central mass; and the anterior extremity is furnished with five diverging cylindrical processes, which advance towards the border of the egg (*e*), two of these, however, disappearing, whilst the other three increase in size, previously to the exclusion of the egg. Either whilst the egg is still within the cloaca, or after it has escaped from the anal orifice, its envelope bursts, and the larva escapes; and in this condition (*f*) it presents very much the appearance of a tadpole, the tail being straightened-out, and propelling the body through the water by its lateral undulations. The centre of the body is occupied by a mass of liquid yolk; and this is continued into the interior of the three anterior processes, each of which has a sort of sucker at its extremity. After swimming about for some hours with an active wriggling movement, the larva attaches itself to some solid body by means of one of these suckers; if disturbed from its position, it at first swims about as before; but it soon completely loses its activity, and becomes permanently attached; and important changes speedily manifest themselves in its interior. The prolongations of the central yolk-substance into the anterior processes and tail, are gradually retracted (*g*, *h*), so that the whole of it is once more concentrated into one mass; and the tail, now consisting only of the gelatinous envelope, is either detached entire from the body, by the contraction of the connecting portion (*i*), or withers and is thrown off gradually in shreds. At this stage, a division of the central mass into two unequal parts is indicated; and the anterior part exhibits a deep yellow annular patch, circumscribing a paler yellow spot, which marks the position of the future mouth; whilst in the posterior portion there is a clear spot, in which the development of the heart commences. The formation of the internal organs takes place very rapidly; so that by the end of the second day of the sedentary state, the outlines of the branchial sac (the mode of whose development has been already described, § 289), and of the stomach and intestine, may be traced; no external orifices, however, being as yet formed. The pulsation of the heart commences on the third day, and the formation of the branchial and anal orifices takes place on the fourth; and the ciliary currents are immediately established through the branchial sac and alimentary canal. It is interesting to remark that the caudate form of the early larva is retained in the curious *Appendicularia*, which in some other particulars

FIG. 247.



Anatomy of more advanced embryo of *Amaroucium proliferum*, showing its progress towards the adult condition;—*a*, general tegumentary envelope; *b*, proper tunic of the individual; *c*, mouth; *e*, branchial sac; *f*, thoracic sinus; *h*, cloaca; *i*, anus; *j*, ganglion; *k*, œsophagus; *l*, stomach; *m*, intestine; *n*, its termination in the cloaca; *o*, heart.

retains the larval type of conformation (§ 289); while the entire form of the young Amaroucium at a later period (Fig. 247) corresponds rather with that of the *Didemnian* group, in which the post-abdomen is not developed, than with that of the *Polyclinians*, which it is ultimately to possess (Fig. 121). The elongation of the posterior portion so as to form the post-abdomen (enclosing the heart and generative apparatus), does not commence until towards the end of the second week; when the formation of the genital organs, from a mass of granular matter between the heart and the intestine, begins to show itself.—The embryonic development of other Ascidians, solitary as well as composite, takes place in a manner essentially the same with the foregoing; a free-moving tadpole-like larva being first produced, in all the instances in which the process has been yet observed; and this attaching itself by some part of its surface, before the development of the future organism has made much progress.*

559. The embryonic development of the *Salpidæ*, however, presents some very curious distinctive features. These animals exist under two distinct forms, the 'solitary,' and the 'aggregate;' every solitary Salpa having an aggregate form, which answers to it and alternates with it. It is in the aggregate Salpæ alone, that sexual organs exist; and each individual contains both ovaria and testes. Nevertheless it seems probable that they are not self-fertilizing; since the development of the spermatic organ has been found in several instances to be more tardy than that of the ovary; so that it is probable that the ovaries of all the zooids of one chain are fertilized by the spermatozoa developed by another. Each zooid usually produces but a single ovum, and propagates but once in life; and this ovum is fertilized whilst yet within the body of the parent, doubtless by spermatozoa drawn-in with the branchial current. Instead of being expelled, however, in an early stage of its embryonic development, the ovum is retained within the body of the parent; and it there forms an adhesion to a peculiar organ, that resembles in all essential particulars, the *placenta* of the Mammal (§ 608), the fœtal and maternal vessels interpenetrating as it were, without communicating, in such a manner as to allow the transudation of fluids from one to the other. The embryo does not become detached, until the greater number of its organs have nearly attained their full development; the alternating pulsations of the heart so characteristic of the class (§ 234), together with the respiratory movements, having been established for some time; and the internal stolon from which the gemmæ are to be put forth, being already present in the form of a short delicate filament, whose edges possess serrations that indicate the points of origin of the future buds.

560. Thus, starting, as before, from the completion of the Generative act, we find a 'solitary' Salpa produced, which, like the first-formed Compound Ascidian, has the power of multiplying its kind by gemmation; and the chief difference between the two cases consists in this, that the original Salpa-stock never evolves true generative organs in its own body, but that these, as in the Hydraform Zoophytes, are developed in distinct

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* In addition to the admirable Memoir of Prof. Milne-Edwards, "Sur les Ascidies Composées," see those of Kölliker ("Ann. des Sci. Nat.," 3e Sér., Tom. V.), Van Beneden ("Mém. de l'Acad. Roy. de Bruxelles," Tom. XX.), Huxley ('On Doliolum and Appendicularia,' "Philos. Transact.," 1851); and Krohn ("Müller's Archiv.," 1852, 1853, translated in "Taylor's Scientific Memoirs").

zooids, which have, like the solitary Salpa, the power of free locomotion, and which thus propagate the race in distinct localities. To speak of the 'solitary' and 'aggregate' Salpæ as constituting two distinct generations, is to affirm that the former are complete organisms; but as they never evolve true generative organs, it is obvious that they have no title to be so regarded, since the evolution of the genital apparatus is essential to the perfection of every fully-organised individual. The character of the species must include, as is now generally admitted, *both* the forms under which it is manifested; and it is necessary to bring together the entire series of vital actions performed by both, in order to possess that complete physiological history of any species of Salpa, which is afforded, in higher animals, by the life of any single individual, if hermaphrodite, or by that of any pair, if diœcious. The production of the 'aggregate' Salpæ must, it is evident, be regarded as a process of *development*, whilst that of the 'solitary' is the only true *generation;* consequently, this example does not, any more than those already cited, afford support to the doctrine of "Alternation of Generations," although usually cited as one of its most characteristic instances.—It is interesting to remark in conclusion, that through the whole of this very interesting group, we find a provision for the *dispersion* of each species, in one state or another of its existence. In the *Ascidians*, it is the embryo which is self-moving, and the adult which is fixed; whilst in the *Salpians*, it is the embryo which is fixed, and the adult which is self-moving. In the one case, as in the other, the motions appear to be purely automatic; but in the embryo they are performed by those simple rhythmical contractions in cellular tissues, which correspond with those of the heart in the early stage of its development (§ 255); whilst in the adult they seem to be reflex, depending on the instrumentality of nerves and muscles.*

561. In the *Conchiferous Acephala* we meet with no indication whatever of the power of gemmiparous multiplication; the true Generative process being the only means by which their reproduction is accomplished, alike in the *Brachiopoda*, and in the *Lamellibranchiata*. In the former of these groups, according to Prof. Owen,† the male and female organs are disposed in distinct individuals; the observations on which this conclusion rests, however, are by no means sufficient to determine this question, as will presently appear. Among the animals of the latter group, also, it has been generally believed in recent years that the sexes are usually separated; spermatozoa having been found in the generative glands of some individuals, and ova in those of others. Hermaphrodism had been recognized, however, in *Pecten*, *Cyclas*, and *Clavagella*, each of these genera possessing distinct testes and ovaria; and from the recent

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* For the most recent information on the Reproduction of the Salpæ, the following Treatises and Memoirs should be especially consulted:—'Observations sur le Génération et le Développement des Biphores,' by M. Krohn, in "Ann. des Sci. Nat.," 3e Sér., Zool., Tom. VI.; "Fauna Littoralis Norvegiæ," by M. Sars, 1846; Huxley 'On Salpa and Pyrosoma,' in "Philos. Transact.," 1851; and Leuckart, "Zoologische Untersuchungen," Heft 2, 1854.—Mr. Huxley's view of the relation of this case to the general theory of 'Alternation of Generations,' exactly corresponds to that which had been previously put-forth by the Author.

† 'On the Anatomy of the Terebratula,' in Mr. Davidson's Monograph on the "British Fossil Brachiopoda" (published by the Palæontographical Society), Vol. I., Introduction, p. 21.

researches of Dr. Davaine* upon the *Oyster*, it appears not improbable that this attribute may be more generally diffused through the group than has been supposed, although there is no ostensible co-existence of two sets of sexual organs. The generative gland of this genus, at the period of reproduction, is very large, surrounding the mass formed by the digestive apparatus, and extending towards the hinge; at other times, however, this organ so completely disappears, that scarcely any traces of it can be detected. This body is sometimes found to contain masses of sperm-cells and spermatozoa, whilst in other instances it is turgid with ova; and hence the conclusion that these animals are bi-sexual, appeared a natural one. Dr. Davaine has met with many instances, however, in which this body contained both spermatozoa and ova, these individuals being consequently hermaphrodite; and he appears to have satisfactorily proved that this hermaphrodism is not an accidental or abnormal occurrence, but that it presents itself as part of the regular history of the genus. For it appears that the spermatozoa are fully evolved, before any trace of ovules can be seen, so that individuals examined in this stage would be accounted *males;* on the other hand, by the time that the ova are fully evolved, the spermatozoa have entirely disappeared, so that individuals examined in this stage would be regarded as *females;* but there is an intermediate period, at which the ova may be distinctly recognized as such, before the spermatozoa have ceased to be distinguishable, being that, probably, at which the fecundation of the ova takes place. The gland seems to be made-up of distinct vesicles, some evolving sperm-cells, and others germ-cells, without any excretory duct; little groups or islets of these vesicles, in which the sperm-cells occupy the interior and the ova the exterior, being enclosed in a network of areolar tissue. By the bursting of the former, and the emission of their spermatozoa, the ova must be fertilized some time before they quit the ovarium. They appear to be set-free from this by the rupture of its envelopes, and to fall into the visceral cavity; from which they find their way (in what manner is not known) to the general cavity of the shell, wherein they are retained until the embryoes have nearly acquired the organization of their parents.—In many Conchifera, a distinct layer of albumen is found between the yolk-membrane and the general envelope; and this is sometimes so considerable in amount, that the yolk-bag forms but a small proportion of the whole ovum.

562. The history of Embryonic Development has been less studied in this class than in most others; and the observations which have been made upon it, are far from possessing the completeness now required by science.† According to the observations of De Quatrefages upon *Teredo*, the first segmentation of the vitellus takes place in the usual manner; but thenceforward the binary subdivision of the two halves goes-on at a very unequal rate. The rapid multiplication of segments in one half, causes these to wrap-round or enfold the other half, even before the latter has undergone any further segmentation; and by a continu-

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* See his 'Recherches sur la Génération des Huitres,' in the "Mémoires lus à la Société de Biologie," 1852.

† See Carus and De Quatrefages on *Anodon*, in "Nova Acta Nat. Cur.," Tom. XVI., and "Ann. des Sci. Nat.," 2^{e} Sér., Zool., Tom. IV., V.; De Quatrefages on *Teredo*, "Ann. des Sci. Nat.," 3^{e} Sér., Zool., Tom. XIX.; and Davaine on *Oyster* (loc. cit.)

ance of the same process, a peripheral layer of cells is formed (reminding us of the outer layer of the blastodermic membrane in Vertebrata), which is destined to be converted into the mantle and its branchial extensions (as well as, probably, into the shell *); whilst the cells which originate in the contained segment, are subsequently metamorphosed into the visceral mass. The superficial cells speedily become covered with cilia; and the embryo, which is at first made to execute a rotatory movement by their vibration, is soon carried freely about by their instrumentality. It cannot be perceived to issue from the envelope of the ovum; but this gradually moulds itself upon its surface, and thins-away, so that the cilia apparently project from its exterior. A cleft shows itself after a time in the peripheral layer, which gradually deepens, and divides it into the two lobes which the mantle thenceforth exhibits. As the development of the permanent organs advances, the cilia of the general surface disappear; but a peculiar bilobed organ, bearing long cilia, is developed from the region of the mouth; and this seems not only to serve as an organ of locomotion, but also (according to Davaine) as the means of bringing food to the mouth, like the rotatory organs of Rotifera. It is represented by the last-named observer as having at first the form of a hollow cylinder, but as becoming gradually narrowed at its base, so as to present more of a funnel-shape; the constriction progressively increasing, until the organ is entirely detached from the body of the embryo. This happens when the cilia clothing the inner surface of the mantle, and also covering the branchiæ, first come into activity; and it is then, too, that the action of the heart and the circulation of the blood first become distinguishable. With the exception of the ciliated organ, the entire embryonic mass seems to undergo a gradual transformation into the permanent fabric of the Mollusk. In the embryo of *Anodon*, there is found, in the angle formed by the junction of the two lateral halves, a short hollow cylinder, the 'organ of the byssus,' from which proceeds a transparent byssus of extraordinary length; and it is remarkable that this organ should be developed in Lamellibranchiata which possess no byssus in the adult condition. The foot is one of the last organs to be evolved, as might be expected, when it is borne in mind that it is an organ belonging to only a part of the group; thus presenting another example of the principle, that the more special condition arises out of the more general.

563. In the *aquatic* orders of the class *Gasteropoda*, we still find the sexes distinct. Among the least active forms of this group, such as the *Patella* and *Chiton*, it is probable that fertilization is effected, as in the Conchifera, without the actual congress of two individuals; but in the higher, the spermatic duct of the male terminates in a projecting organ, adapted to convey its fluid within the oviduct of the female. In the aquatic Gasteropoda possessing spiral shells, the ovary in the female and the testes in the male occupy a corresponding position,— the higher part of the cavity of the shell. In the *Paludina vivipara*, the ova are delayed in a dilatation of the oviduct near its extremity, until the young

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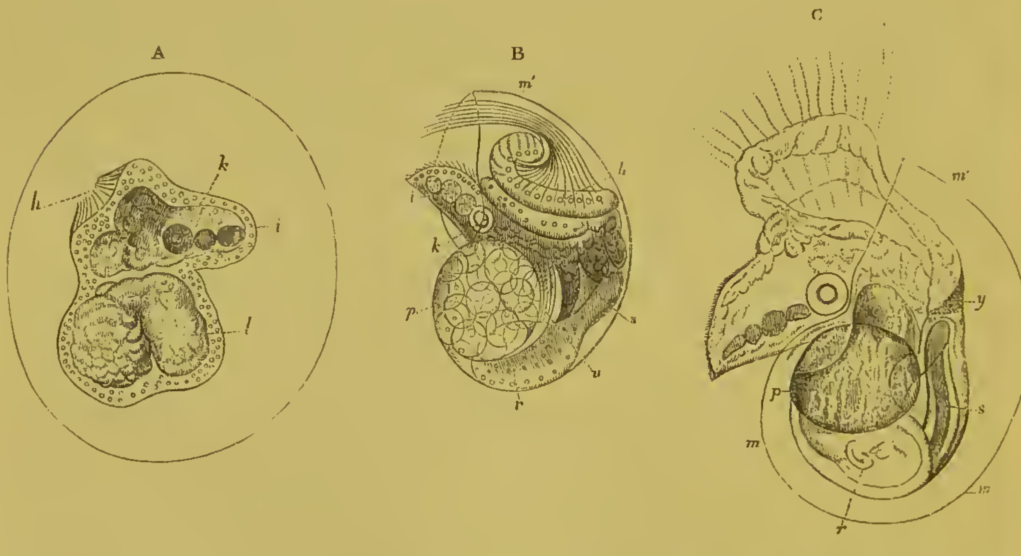
* It is affirmed by De Quatrefages (who accords on this point with Serres), that the bivalve shell is formed by the calcification of the 'ovarian envelope,' or vitelline membrane, of the ovum. The Author cannot but believe, however, that there has been some error of observation or of inference upon this point; and that the shell is formed by the calcification of the outer layer of the cells of the embryonic mass.

are so completely matured, that they are hatched there, so as to pass out alive; but in most, if not in all, other cases, they are deposited by the parent, before the development of the embryo has proceeded far. Frequently, however, they are provided with an additional protective covering or *nidamentum*, which is formed by large glands situated near the termination of the oviduct. This 'nidamentum' has different forms in the several species which produce it. In some instances it is a sort of gelatinous mass, in which the ova are imbedded with greater or less regularity; such masses are attached by the common *Lymnæus* to water-plants; but those most remarkable for size and regularity are deposited by the *Nudibranchiata*. Thus Mr. Darwin speaks of one produced by a *Doris* of the Falkland Islands about 3½ inches long, which measured nearly twenty inches in length by half an inch in breadth; and which, on a moderate computation, must have contained 600,000 eggs, a number which is far from being without parallel in these most fertile animals. But in general the nidamentum is composed of a large number of distinct sacs, each containing a few eggs; and these are connected together by a sort of footstalk. In the common *Buccinum undatum* (whelk), these sacs are flattened spheres, and are united together in the manner of bunches of fruit; very large masses of them are often to be picked-up on our shores. In the *Pyrula*, they are flattened disc-like cases, united into a single string by a pedicle connecting the centre of each disc with that of the next.—The *pulmoniferous* Gasteropoda, on the other hand, are hermaphrodite, each individual possessing male and female organs; they are not usually capable, however, of self-impregnation, the congress of two being necessary, and each fertilising the ova of the other; yet it has been lately observed, in several instances, that individuals of *Lymnæus stagnalis*, reared solitarily from the egg, have produced fertile ova. The eggs of these species are deposited singly in the earth, and are hatched by the warmth of the sun; and they are capable of being dried-up or frozen without the loss of their fertility.—The Generative apparatus in the active little *Pteropoda* nearly resembles that of the pulmonated Gasteropods; the male and female organs are united in the same individual, but the congress of two is required. In the *Clio*, which alone has been minutely examined in this respect, the male organs are of very large size; the testis occupying a great part of the cavity of the body, and the penis being of extraordinary length.

564. The history of the Embryonic development of Gasteropoda presents a series of facts of great interest; and as this class may be considered as the type of the Molluscous group, we may probably regard the course of its development as that which is most characteristic of the sub-kingdom as a whole. Numerous and valuable observations have been made upon the evolution of the ova of various members of the class, both 'testaceous' and 'naked;' and it may be stated as their uniform result, that the young of the latter, as well as of the former, are provided with a simple spiral shell at their exit from the egg, although they may subsequently cast this off; and further, that the young of the aquatic species are provided with instruments for locomotion, which they do not possess in their adult condition; the obvious purpose being here, as in other cases, to disperse them over a wider area than that through which the sluggish movements they perform in their perfect state would enable them to extend.—The ova of Gasteropoda generally contain a considerable amount of albumen, sur-

rounding the vitelline sac; and this is subsequently absorbed into the embryonic mass, in proportion as the material directly supplied by the yolk is exhausted. The most minute account yet given of the embryonic development of any Gasteropod, being that of M. Vogt, whose observations were made upon *Acteon viridis*, one of the Nudibranchiate order, it will be from this source that the following sketch will be chiefly derived.—The early changes which the yolk undergoes, are conformable in all essential particulars to the ordinary type; save that, as in the Conchifera, the process of segmentation divides it into unequal instead of equal parts; and that in this mode, a distinction is very early manifested between a peripheral layer of small cells, and the included mass of which the cells are much larger. It is not certain, however, that this peculiarity is common to Gasteropods generally. When the subdivided yolk has attained the condition of the 'mulberry mass,' a curious alternating revolution begins to takes place in this body, within the egg; two or three turns being made in one direction, and the same number in a reverse direction. This movement, which seems due to ciliary action, may be well observed in the ova of the common *Lymnæus stagnalis*, in which it continues during a large portion of the period that elapses before the escape of the embryo from the ovum. The embryonic mass soon begins to show a bi-lateral symmetry; and before very long, a subdivision is indicated into the anterior or cephalic portion, and the posterior or visceral. The parts which are first developed, are by no means those which are most characteristic of the adult; for the cephalic portion is soon extended on each side into a lobe bearing a superficial resemblance to the fin-like expanse of the Pteropoda (Fig. 46), which is furnished with long cilia (Fig. 248, *h*); it is also observed to contain the auditory vesicle, or rather its 'otolithe' (*k*),

Fig. 248.



Development of embryo of *Acteon viridis*, as seen in the lateral aspect:—A, at the end of the fourth day; B, seventh day; C, twenty-fifth day; *h*, rotatory organs; *i*, foot; *k*, auditory vesicle; *l*, ventral portion of the embryo; *m m′*, shell; *p*, liver; *r*, stomach; *s*, intestine; *u*, suspensor muscle; *y*, black pigment of the hood of the mantle.

which, although so early developed, remains in the same rudimentary state during the whole of life; and it is from this part, also, that the prominence (*i*) is put forth, which is afterwards to be evolved into the foot or muscular disk of the animal. The formation of these parts has made considerable progress by the end of the fourth day after the deposit of the fertilized ovum, when the ventral portion of the embryo merely consists of a mass of cells, in which not even the outline of its future organs can be seen, though a breaking-up of the mass into groups of cells begins to show itself. On the next day, the shell first makes its appearance, as a very thin layer over the lower part of the ventral mass; and this extends itself on subsequent days, until, by the eighth, it becomes large enough to enclose the embryo completely, when the latter contracts itself (B, *m m′*). During this period, the formation of the internal organs is rapidly taking place; for at its termination, the stomach, *r*, and intestine, *s*, are clearly distinguishable, as is also the suspensor muscle, *u*; but the liver, which is so important and characteristic an organ in this group, exists only as a mass of untransformed cells (*p*). The movements of the embryo now change their character; it projects itself from the shell, expands its ciliated lobes (Fig. 48), sets the cilia in vibration, and after a while draws itself into its shell again, very much after the manner of a Rotifer or a Bryozoon; and when it is completely retracted, the foot closes the orifice of the shell, like an operculum. It is curious to trace the regular rhythmical movement of *rotation* gradually giving place to these less constant and apparently more spontaneous actions. At the period when the embryo is ready for emersion, its movements have become as active as the narrowness of its prison permits; and when it is set-free by the rupture of its envelope, it swims-forth by the action of its ciliated lobes, these also serving to bring food into its mouth, which does not possess at this period any trace of the reducing apparatus subsequently to be developed. Its condition at that time is seen at C; the principal change from the state shown in the preceding figure, being in the condition of the liver, which is now in progress of transformation into the perfect type. The 'mantle,' also, is now very distinct from the subjacent parts.

565. The subsequent history of the process has not been fully traced out; but it is doubtless in this earlier portion, that its chief peculiarity consists. The transformation of the entire yolk into the substance of the embryo, and the origination of all the organs of the latter in the cells that are formed by the subdivision of the former, is doubtless a very important feature in the process. The order in which the organs are evolved,—the ciliated lobes and foot, the otolithes and auditory vesicles, the shell, the mantle and operculum, the liver and intestine,—is also extremely remarkable. But the most curious fact of all, and the one which is most significant of the predominance of the organs of *vegetative* over those of *animal* life, in this group, is the *entire absence* of all trace either of Nervous or Circulating systems, at a time when the general structure of the embryo, and especially the visceral apparatus, has made such great progress, as to enable it to lead an active life, and to digest and assimilate its own food immediately on its emersion from the egg. Further it may be observed in the course of this development, that the progress from the general to the special is on the whole extremely well marked; the difference being first manifested between the containing and the contained parts, then

between the cephalic and visceral, and then between the several groups of cells into which the component mass of the latter breaks-up, each taking-on its own distinct method of evolution.

566. A very curious phenomenon has been noticed by several observers, which seems like an imperfect gemmiparous production in the early embryo. It is not unfrequently seen that some of the cells of the vitelline mass detach themselves from the principal cluster, become clothed with long cilia, and continue to move-about actively within the egg, until the escape of the embryo. It is even affirmed by Nordnann, that they increase by partial subdivision, and that thus from a single detached cell may be produced a cluster, having a very definite form, and furnished with long cilia, so as very strongly to resemble a parasitic animal. It has not been shewn, however, that these bodies ever advance to a higher condition, or are capable of generating their kind; and the correct view is probably to regard them (with Vogt) simply as portions of the embryonic mass, exactly resembling those that form the ciliated lobes, which, being detached from the rest, preserve their vitality for an unusually long time; such vitality, however, not being different in kind from that of an ordinary ciliated epithelium-cell, though greater in degree.—It is affirmed by Agassiz, however, that the vitelline mass sometimes divides itself spontaneously into two portions, and that each of these may become a perfect animal; which statement, if correct, adds confirmation to the doctrine already put-forth (§ 480) respecting the origin of double monsters. On the other hand, in certain *Pectinibranchiata* (if there be no fallacy in the recent observations of MM. Koren and Danielssen), several vitelline masses—even to the number of a hundred or more—developed from distinct ova, coalesce to form a single embryo; a phenomenon which, so far as is at present known, has no parallel, either in the Animal or in the Vegetable kingdom.*

567. All the species of the class *Cephalopoda*, so far as is at present known, are diœcious, the male and female organs being disposed on separate individuals. There is, nevertheless, a remarkable similarity between these organs, both in their general aspect, and in certain peculiarities which they present. The testis of the male consists of a capacious membranous sac, which, when opened, is found to contain a mass of short branching cæca, attached to a small portion of its inner surface; these cæca, however, have not any orifice for the discharge of their secretion, which appears to escape into the general cavity by the rupture of their walls. From this cavity it is conveyed by a duct, which, after passing through other accessory glandular structures, enters a wide muscular sac, where a remarkable change is effected in the condition of the spermatozoa. A number of them are clustered together, and enclosed in peculiar investments, which are known under the name of *spermatophora* or *the moving filaments of Needham*, and which are obviously analogous to the nidamental investments of the ova in the female. These are from half to two-

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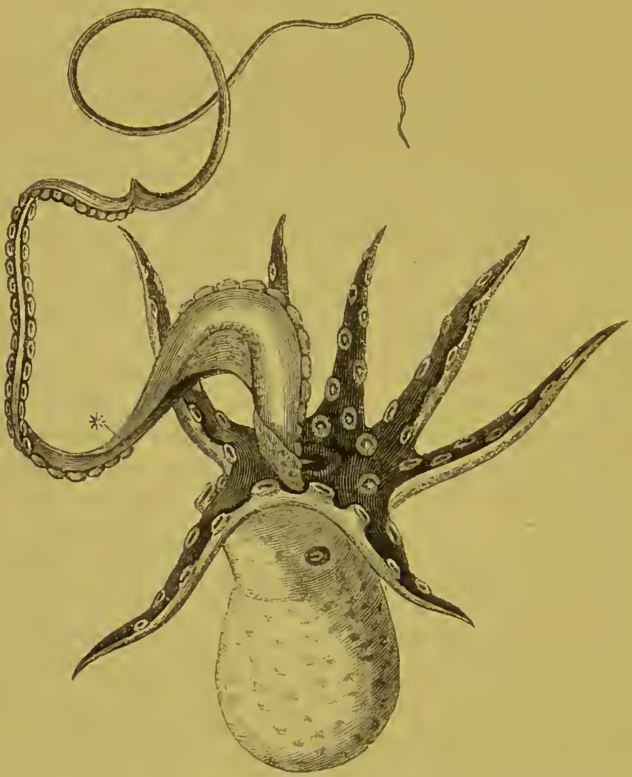
* On the Embryology of the Gasteropoda, see especially the admirable Memoir of M. Vogt, in the "Ann. des Sci. Nat.," 3e Sér., Zool., Tom VI., and the various preceding Memoirs there referred-to; the Memoir of M. Nordnann on *Tergipes*, Op. cit., Tom. V.; the Lectures of Prof. Agassiz on "Comparative Embryology;" and the Memoirs of MM. Koren and Danielssen, on the development of *Buccinum undatum* and *Purpura lapillus* in "Ann. des Sci. Nat.," 3e Sér., Zool., Tom. XVIII., XIX.

thirds of an inch in length; and each consists of an external, transparent, and cylindrical case, in which is contained the proper sperm-sac. A little more than the anterior third of this is spirally disposed, and to this part Needham applied the term *screw;* next follows a short portion, which he calls the *sucker;* then a still smaller and cup-shaped part; and lastly an oblong and spongy bag, in which are contained the minute spermatozoa. When moistened with water, these bodies commence a series of alternate contractions and relaxations, by which the filament within is moved forwards, and the screw with its compressed spire is thrust forcibly against the anterior part of the capsule. This capsule in a short time becomes ruptured; by degrees the cup and sucker advance; and, as soon as they have escaped from the end of the cylinder, the spongy tail is forcibly driven out, and generally with so much violence as to break it into several pieces, thus giving exit to its contained spermatozoa. These movements are certainly not caused by the exercise of any distinctly-animal powers residing in the spermatophora; but they are partly dependent upon the peculiar properties possessed by the membranes and filaments in relation to water, for they are exhibited long after the death of the Cephalopod, if the filaments be taken out of the sac and placed in that fluid. Their function is thus evidently to diffuse the spermatozoa through the surrounding medium, in such a manner that they may find their way into the midst of the large clusters of ova deposited by the female; these are probably fertilized after their extrusion from her body (as in Fishes and Batrachia), since, in most species at least, the intromittent organ does not seem long enough to convey the fecundating fluid within it. As to the degree of actual congress between the sexes, there are various accounts, probably relating to different species.—The ovarium of the female, like the testis of the male, consists of a large sac with thickened walls; and, if this be opened at a time when the ovules are in an advanced stage of development, it will be found to contain a cluster of little egg-shaped bodies, attached to a small part of the inner wall of the sac, by short pedicles which principally consist of blood-vessels. These bodies consist of a portion of the substance of the sac, with its lining membrane, raised-up by the development of the ovisacs; and each of them contains an ovule, which, when ready for extrusion, escapes, by the gradual thinning and final rupture of its envelope, into the general cavity. The ruptured membrane remains in the form of a cup; and we thus witness in this class the first appearance of the *calyx,* which is developed from the external surface of the ovarium in the oviparous Vertebrata (§ 597). From the cavity of the ovarium proceeds the oviduct, which conveys the ova into a glandular body, where they receive a nidamental investment, the nature and form of which differ in the various species. It may be specially mentioned, however, that the shell of the *Argonaut* (Paper Nautilus) is very probably to be regarded in the light of a nidamental receptacle for the ova; as it is peculiar to the female of that animal, and the eggs are attached to its involuted portion by long filamentary stalks. The vitelline sac is not surrounded (as in Gasteropoda) by a layer of fluid albumen, but is immediately invested by the chorion or general envelope.

568. The generative process is performed, on the part of the male *Argonaut,* as well as on that of some other *Octopods,* in a most remarkable

and apparently-exceptional manner. One of the arms, instead of being developed like the rest, at first lies coiled-up within a sac, which is attached to the body by a peduncle in the position which the arm would occupy; its movements may be readily distinguished on the exterior; and at last these become so violent that the sac ruptures, and the arm extends itself, bearing the remains of the sac (now everted) as a sort of fringe (Fig. 249). This arm differs externally from the rest, not merely in the greater length and diameter of its sucker-bearing portion, but also in being furnished with a peculiar whip-like prolongation, which bears no suckers; internally its structure is essentially the same with that of the other arms, possessing the same arrangement of muscles and nerves in connection with the suckers, but being also furnished with a seminal duct, which is prolonged from the testis contained within the body of the animal, to nearly the extremity of the whip-like appendage, and is dilated in one part of its course into a sac. At a certain epoch of development, this arm is cast-off, and becomes an independent zooid, moving through the water by its own muscular contractions, somewhat after the manner of a worm; and the seminal sac and ducts are then found to be filled with a substance resembling a bundle of threads, which, when examined microscopically, is found to be composed of an aggregation of spermatozoa. In this condition the detached arm was long since observed by Della Chaje, and was supposed by him to be a parasitic worm; and it

Fig. 249.



Male *Argonaut*, showing the *Hectocotylus*-arm after its escape from the investing sac; at * is seen the extremity of the double fringe formed by the everted membrane of the sac.

was subsequently described by Cuvier, who also considered it as a complete animal, under the name of *Hectocotylus.* Having been brought by its movements into contact with a female of its own species, the Hectocotylus-arm forthwith effects the impregnation of its ova, insinuating its filiform prolongation, in the manner of a penis, into the oviduct. How long the Hectocotylus-arm may continue to live after its detachment, is not yet known; but since it has no organs of digestion, and is therefore destitute of the power of assimilating food for itself, and since it contains no testis, and must therefore be incapable of secreting a fresh supply of semen in place of that which has been discharged, it seems probable that its independent existence is not prolonged after its generative function has been once performed. In fact, we may regard this strange modification and detachment of the Hectocotylus-arm, as answering the purpose of the spermatophore of other Cephalopods; for although the whole seminal product contained in the body of the Hectocotylus is enclosed in one enormous spermatophore, this does not seem to possess any self-moving power; and it is not by its means, therefore, but by the movements of the Hectocotylus which encloses it, that the spermatozoa are brought into the necessary proximity with the ova to be fertilized. Whether the male Octopus reproduces the Hectocotylus-arm after its detachment, has not yet been determined; the probability, however, seems strongly in favour of its doing so.*

569. The history of the Embryonic development of the Cephalopoda, which has been very carefully studied by Prof. Kölliker,† differs in many important particulars from that of the lower Mollusca; and these are, for the most part, characters of approximation to the Vertebrata. For, in the first place, the process of segmentation does not take-place in the whole yolk, but only in the portion of it nearest to the embryonic vesicle; and from this arises a cluster of cells, which lies upon the surface of the yolk, and sends-out an extension all around. This extension, the representative of the 'germinal membrane' of the Fowl's egg, constitutes the yolk-sac; whilst from the original cluster, or at least from the cells of its outer layer, are produced the several organs of the embryo. Thus, when the process of development commences, the first structures are seen rising-off (so to speak) one end of the yolk-sac; but as they gradually draw to themselves and appropriate the substance of the yolk, the embryonic mass increases, and the yolk-sac diminishes; until at last, at the time of the emersion of the embryo from the egg, the contents of the yolk-sac being nearly exhausted, it presents itself as a mere appendage to the embryo.—The mode and order of appearance of the principal organs, are very

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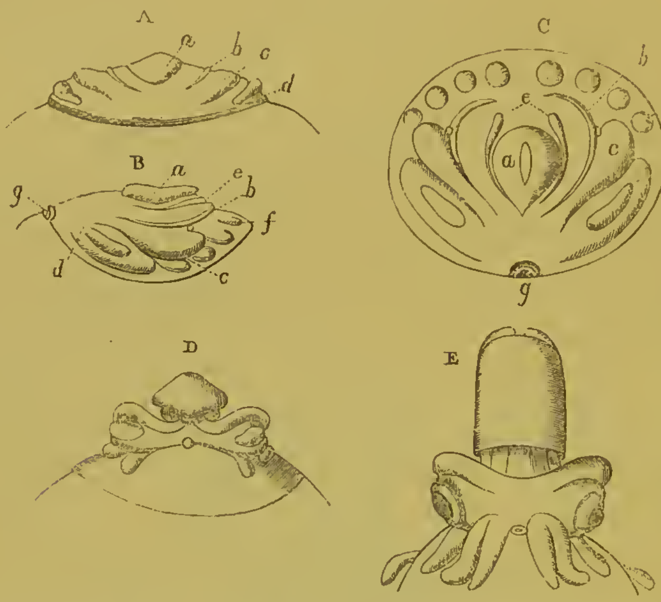
* It was by Prof. Kölliker, that the Cephalopod nature and sexual function of the Hectocotylus were first asserted; he fell into the mistake, however, of supposing it to be an entire animal (being partly led to this idea by some erroneous statements as to its development, furnished to him by Mad. Power); and his account of its anatomy was given under the erroneous influence of this preconception (see "Annals of Nat. Hist." Vol. XVI., 1845, "Linnæan Transactions," Vol. XX., and "Bericht von der Königlichen Zootomischen Anstalt zü Wurzburg," 1849.) The first idea of the truth was promulgated by Verany in his "Mollusques Mediterranéens," 1° partie, p. 128; and the completion of the proof has been afforded by his own researches in conjunction with those of M. Vogt ("Ann. des Sci. Nat.," 3^{e} Sér., Zool., Tom XVII.), and by those of Prof. H. Müller ("Siebold and Kölliker's Zeitschrift," June 1852). The two last-named memoirs are translated in "Taylor's Scientific Memoirs," Natural History, 1853.

† "Entwickelungsgeschichte der Cephalopoden;" Zurich, 1844.

different from what we might expect. The first part of the germ-mass that becomes distinct, is a slight central elevation, which is afterwards to become the visceral portion, covered with its mantle (Fig. 250, A, B, C, *a*);

FIG. 250.

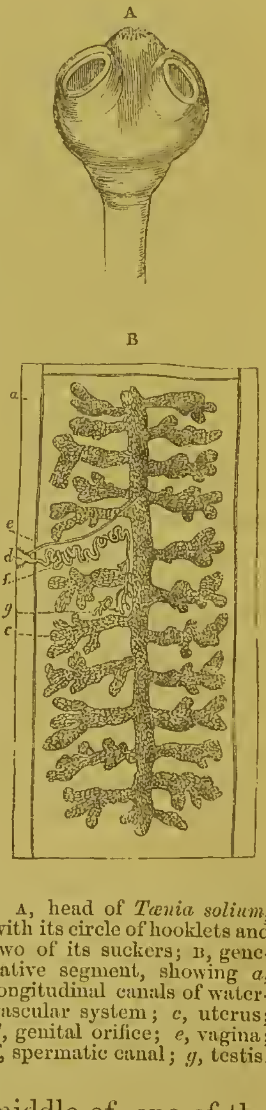


Successive stages of Development of *Sepia:*—A, B, C, first appearance of permanent parts at the extremity of the yolk-sac, as seen end-ways, side-ways, and from above; *a*, mantle; *b*, funnel completely divided in half; *c*, inner, and *d*, outer cephalic lobes; *e*, branchiæ; *f*, arms; *g*, mouth:—D, more advanced embryo, beginning to rise from the surface of the yolk-sac:—E, embryo beginning to present the form of the perfect animal.

around and beneath this, on either side, is an elevation (*b*) that subsequently forms half of the funnel, the two halves being at first widely separated from each other; and around this, again, is a bilobed expansion (*c*, *d*) which forms the cephalic portion, each lobe bearing one of the eyes, and sending-off from its under side (that nearest the yolk) as many projections (*f*) as the species is to possess arms. The position of the mouth (*g*) is indicated at the junction of these two lobes. Gradually the visceral portion becomes more elevated from the surface of the yolk-sac (D), by the augmentation of its own substance; and in so doing, the two halves of the funnel approximate each other until they join. The mantle becomes very distinct from the included parts, and is extended posteriorly into a fin-like organ on either side. The cephalic lobes are still (like those of Gasteropoda) very large in proportion to the rest of the body; and the eyes which they bear are very early developed in these animals, as if for the purpose of guiding their active movements on their emersion from the egg (E). The arms increase in length, extending themselves over the yolk-sac, which they seem (as it were) to embrace; and thus the peduncle by which it is connected with the embryo, comes to be nearly in their centre. The development of the various organs in the visceral mass takes-place in an order much nearer to that of Vertebrata than to that of Gasteropoda; for the evolution of the circulating and permanent respiratory apparatus goes-on *pari passu* with that of the digestive; and that of the nervous system is not far behind. At the time of the escape of the common *Sepia* from the egg, the first layers of its shell are found between the folds of the mantle in the dorsal region; the ink-bag is charged with its characteristic secretion: nearly all the organs characteristic of the adult are distinguishable, though not as yet in their relative proportions; and the young animal is capable of swimming actively through the water, both by means of its lateral fins, and by its cephalic arms, which are furnished with a connecting web that remains permanent in some species. The yolk-bag is not yet completely emptied, and it is found in the midst of the circle of arms, communicating with the stomach by a duct that passes-down parallel to the œsophagus; it is gradually emptied and drawn-in, however, and its original connection is only indicated by a cæcal protrusion from the anterior part of the 'crop.'—This is the first example we have yet encountered, in which the embryonic development is so far completed within the egg, that the young animal comes-forth in the general condition of its parent; and it seems obviously connected with the fact, that the yolk is here formed in much larger proportional amount; so that it serves, not merely to supply the materials for the production of the first embryonic mass, but also for its continued growth, and for its evolution into the several organs characteristic of the adult form.

570. We now return to a much simpler order of phenomena, that is presented to us in the inferior part of the *Articulated* series; in which we find an almost complete reversion to the Zoophytic type, as regards the repetition of similar parts in the segments of the body, the formation of these by successive gemmation, and their power of independent existence. This is especially seen in the lowest *Entozoa*, the simplest of whose forms (such as the *Gregarina*, § 530) carry us back to the type of the Protozoa; in which multiplication takes-place by mere cell-division, every product of such division repeating the original form, and being able to live detached from the rest; whilst the proper Generative act is one of simple conjugation.—In the *Cestoid* Entozoa, however, notwithstanding the very imperfect development of their nutritive system (§ 138), the Generative apparatus presents a most remarkable evolution. Their so-called 'body' is, indeed, nothing else than a longitudinal repetition of generative segments, each of which contains both sets of sexual organs, and appears to be self-fertilizing. The testis or spermatic organ, in the *Tænia* (Fig. 251, B, *g*), is of comparatively small size, and occupies the centre of the segment; its product is conveyed by the convoluted spermatic duct (*f*) towards the genital pore (*d*), which is seen in the middle of one of the margins, usually alternating from one side to the other in successive seg-

FIG. 251.



A, head of *Tænia solium*, with its circle of hooklets and two of its suckers; B, generative segment, showing *a*, longitudinal canals of water-vascular system; *c*, uterus; *d*, genital orifice; *e*, vagina; *f*, spermatic canal; *g*, testis.

ments. In the same spot we find the termination of what is commonly accounted the oviduct, but which really seems rather to be compared to a vagina (*e*); this leads to a spermotheca, or dilated receptacle for the seminal fluid, as also to the ovary. This last organ, in other Cestoidea (and probably also in the Tænia), is composed of two distinct parts, opening by separate canals; one of these furnishes the germinal vesicles, while the other supplies the substance of the yolk. The ova, after being fertilized, pass by a wide canal into the large ramifying uterine cavity (usually designated the ovarium), which occupies the greater part of each segment (*c*, *c*); and there they remain until mature. It is not yet certain whether the ova pass-out by a special aperture, or whether they are set-free by the bursting of the segment, which previously detaches itself from the body, like the seed-vessel of a Plant.—These generative segments are successively budded-off from the anterior segment or 'head,' and also multiply in the first instance by their own subdivision; as the development of their sexual organs proceeds, however (this being of course most advanced in the segments furthest removed from the head), the whole *nisus* of each segment seems concentrated upon it, and no further multiplication by subdivision takes place, though the budding-off of new segments from the head continues. At the same time, the terminal segments, as their ova arrive at maturity, are detached in their turn; and thus a constant succession is kept-up, which very closely resembles the development and detachment of the Medusa-buds of the Hydraform Zoophytes (§ 543).

571. The investigations which have been recently made by Profrs. Siebold, Van Beneden, and others, into the Development of the Cestoid Entozoa, though far from being yet complete, have evolved several facts of extreme interest. It may now be considered as well established, that the *Cystic* Entozoa (such as the Cysticercus, Echinococcus, and Cœnurus) are nothing else than *Cestoidea* in an imperfectly-developed state; their bodies being encysted in the caudal segment, and this being (as it were) dropsically distended. The very same embryoes, in fact, may evolve themselves into the Cystic or into the Cestoid form, according to the circumstances under which they are placed; for when lodged in the *parenchyma* of organs, such as the brain or the liver, they take the Cystic form; when they pass, on the other hand, into the intestinal canal, their generative segments are developed, and they become Cestoids. It is among herbivorous animals, that the parenchymatous organs are most commonly infested with Cystic entozoa; whilst the alimentary canal of carnivorous animals, into which the flesh containing these parasites enters as food, affords the nidus within which the worm acquires its complete development as a Cestoid. For it is only then that the generative apparatus is evolved, and that eggs are set free, which find their way into the bodies of the vegetable-feeders; although in the Cystic form in which they there develope themselves, a multiplication by gemmation may occur to a very considerable extent. Some parasites of this order, moreover, develope themselves under the Cystic form in Mollusks and cold-blooded Vertebrata; and only evolve their generative apparatus, when transferred from the bodies of these into the intestinal canal of warm-blooded Vertebrata. These results have been obtained by a laborious investigation and comparison of the Entozoa which infest the animals that prey one

upon another; and they may now be considered as well established, though in the history of some of the Cestoid Entozoa (as the *Tænia* which infests Man) much still remains to be cleared-up. From the recent observations of Prof. Van Beneden, it appears that the embryo *Tænia*, at the time of its emersion from the egg, is a minute ovoid body (scarcely exceeding the red corpuscle of the Frog's blood in size), possessing six hooks; and that these hooks, first uniting together, make their way into the tissue on which the embryo may lie, and then, separating and curving backwards, force the body into its substance: but observers are not yet agreed, with regard to the mode in which this embryo becomes a *Tænia* or a *Cysticercus*. The development of the *Tetrarhyncus*, however, has been more fully elucidated. The embryo, which is at first an ovoid sac, provided anteriorly with four lobes, but having no trace of uncinated proboscides, undergoes a sort of self-invagination; the head becoming retracted within the dilatable posterior extremity, which invests and incloses it. This invagination is not permanent at first, though it soon becomes so, if the worm have worked its way into any of the parenchymatous organs or sub-serous membranes; and in addition, the animal secretes, and becomes invested by, a transparent cyst. It is while the worm is in this condition, that its proboscides attain their full development; and after a time the hinder end of the included head spontaneously separates from the wall of the vesicular portion, so that the former lies free and independent within its own body, the latter being again invested by its secreted cyst. There is no evidence to show that the encysted Tetrarhyncus ever undergoes any higher development; but if the Mollusk or Fish in which it is parasitic, be devoured by some predaceous Fish or Bird, so as to bring the Tetrarhyncus into its normal habitat, its development will then proceed; for the cyst being dissolved by the digestive process, the liberated body lengthens posteriorly so as to form a sort of tail, which soon becomes divided into well-marked articulations, the number of which is continually increased by a process of gemmation from the posterior extremity of the head, as already described in regard to the Tænia.*

572. Although the *Trematode* Entozoa do not present, like the Cestoids, a succession of distinct generative segments, yet their generative apparatus occupies a very large part of the body, as shown in Fig. 252. Both kinds of sexual organs are present in each individual; and it is probable that they are self-fertilizing. The male organs in *Distoma hepaticum* (Fluke) consist of a set of extremely long and convoluted seminiferous tubules, occupying the central part of the body; and these discharge part of their secretion by two trunks into a common canal, which terminates in the penis or intromittent organ, situated just behind the anterior sucker. The organs which are commonly termed the ovaries, and which form in the Distoma a large racemose mass that occupies the sides and posterior part of the body, serve really but to furnish

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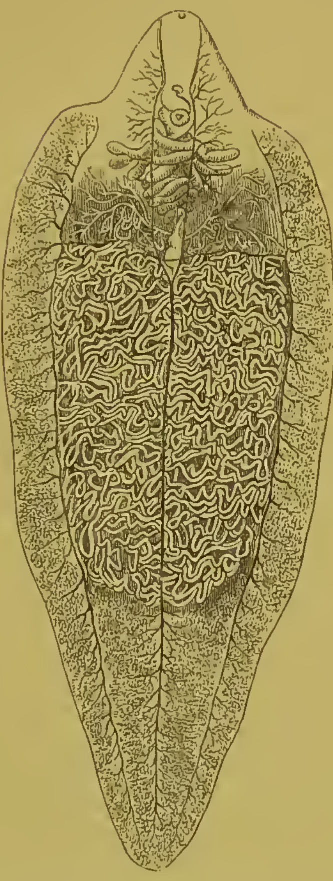
* See Siebold 'Uber der Generation's-wechsel der Cestoden,' in Siebold and Kölliker's Zeitschrift," July, 1850, translated in "Ann. des Sci. Nat.," 3e Sér., Zool., Tom. XV., and 'Expériences sur la Transformation des Cysticerques en Tænias,' in "Ann. des Sci. Nat.," 3e Sér., Zool., Tom. XVII., Van Beneden "Les Vers Cestoides ou Acotyles," Bruxelles, 1850, and 'Nouvelles Observations sur le Développement des Vers Cestoides,' in "Ann. des Sci. Nat.," 3e Sér., Zool., Tom. XX.

the vitelline cells; they open by two canals anteriorly into the uterus, which also receives the ducts proceeding from a pair of smaller dendritic organs, within which the germinal vesicles are evolved. The ova are therefore formed within the uterus by the union of these two essential components; and it seems probable that they are there fertilized, when no congress of two individuals takes place, by seminal fluid directly conveyed from one of the testes by a special duct terminating in a vesicula seminalis. The uterus has a vaginal outlet, however, which opens in close apposition to the penis; so that there seems to be a provision alike for the mutual impregnation of two individuals, and for the self-fertilization of a solitary one.*—The history of the Development of the Trematoda presents a number of very curious phenomena; the process of 'larval gemmation' (analogous in some degree to that of Echinodermata) being repeated two or three times, before the characteristic form of the animal is evolved. In no instance has the entire series of phases through which any one species thus passes, been consecutively watched; but the following will serve as an example of what is believed to occur in certain of these Entozoa. The ovum of the *Distoma* which inhabits the *Lymnæus stagnalis*, is first developed into a little worm-like body, in which no complete organs are evolved, but which seems to consist of the cellular 'germinal mass' inclosed in a contractile integument. Its component cells are in their turn developed into independent zooids, which escape from the enveloping cyst, and from the animal on which it is parasitic, in the condition of free ciliated animalcule-like bodies, or *Cercariæ;* in this condition they may remain for some time, and then they imbed themselves in the mucus which covers the tail of the Mollusk, in which they undergo a gradual development into true Distomata; and having thus acquired their perfect form, they penetrate the soft integument, and take up their habitation in the interior of the body. Thus a considerable number of Distomata may be produced from a single ovum, by the separation of the first products of the sub-division of the embryo-cell.—A most remarkable phenomenon has recently been observed in a Trematode Entozoon, which has long been considered as a Physiological curiosity; namely, the *Diplozoon paradoxum*, a parasite upon the gills of certain Fishes. This animal has been until lately regarded as possessing two

Fig. 252.



Generative Apparatus of *Distoma hepaticum* (Fluke):—in the central portion are seen the testes, composed of convoluted tubuli; in front of this are the arborescent glandular bodies that furnish the germinal vesicles, whilst at the sides and posterior part of the body are the racemose masses that supply the vitelline cells; between these, anteriorly, is the uterus containing ova arrived at maturity.

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* This, indeed, seems to hold good even with certain Pulmonated Gasteropods (§ 563).

complete bodies united only by a narrow band; each body having its own mouth and digestive organs, its own water-vascular system, and its own double generative apparatus; but the stomach and vessels of the two halves communicating freely with each other through the connecting bridge; the whole thus bearing a close resemblance to those 'double monsters' which sometimes present themselves among higher animals. The constancy of the recurrence of precisely the same form, however, was quite sufficient to indicate its normal character; and the source of the duplicity is now known to lie in the 'conjugation' of two previously independent individuals, which become partially 'fused' into each other. This conjugation appears to have reference to the evolution of the generative apparatus; for previously to its occurrence, the Entozoon (known in its single form under the name of *Diporpa*) is destitute of sexual organs.*

573. The *Planariæ* (now referred to the group of Turbellaria) present an arrangement of the generative organs, that bears a strong resemblance to the foregoing. The testes (Fig. 101, *g*, *g*) lie one on each side of the stomach, and pour their secretion into the central receptacle or vesicula seminalis (*h*), from which proceeds an efferent canal that terminates in a penis (*i*). The ovaries would seem to be much more extensively diffused; in fact, ova may be seen in nearly all the spaces not occupied by other organs; and it would hence seem probable that the ovary sends ramifications, commencing in the dilated oviducts (*k*, *k*), into almost every part of the body. The oviducts unite in a dilated cavity (*l*), which is perhaps a spermotheca; and from this there is an outlet by a short wide canal (*m*). It is certain that a sexual congress occurs among these animals, and that they may mutually impregnate one another; but it is probable that they are also self-impregnating, like the Cestoid and Trematode Entozoa.—The development of the ova in *Planariæ* presents several curious features; one of the principal being, that the 'germinal mass,' like that of Distoma, separates into a (variable) number of segments, each of which developes itself into a distinct Zooid.†—The *Planariæ* are scarcely less remarkable than is the Hydra itself, for their capacity for being multiplied by artificial scission; and it is not unlikely that they may undergo a spontaneous separation of this kind, more especially as such fissiparous multiplication is normally exhibited among some other members of the same group, such as the *Nemertinæ*. No production of detached gemmæ, however, is known to occur among them.

574. In the *Nematoid Entozoa* (Ascaris, Strongylus, &c.), on the other hand, the Generative apparatus is arranged upon the diœcious type; the male and female organs being peculiar to distinct individuals, and the ova being fertilized by sexual congress. The male genital apparatus usually consists of a single long tube, enlarged at its lower part into a vesicula seminalis, and terminating in an intromittent organ or penis, which is sometimes of considerable length. The female ovary, on the other hand, sometimes consists of a single tube very much prolonged (Fig. 52, *e*, *e*, *e*), whilst in other instances it is double or multiple; in either case, however, it opens into a wide oviduct, which has frequently a uterine dilatation (*f*) near its termination, whence proceeds a vaginal

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* See Prof. Siebold, in "Siebold and Kölliker's Zeitschrift," March, 1851.

† See Prof. Siebold in "Vergleichende Anatomie," Band I., § 129.

canal, whose external orifice (*h*) is usually at some distance from the anus, and is frequently in the middle or even (as here) in the anterior portion of the body. The male is almost always smaller than the female, sometimes very much so; and when, in the sexual congress, his anal extremity attaches itself to her genital orifice, he has the appearance of a branch or young individual sent-off by gemmation, and attached at an acute angle to the body.—In the *Syngamus trachealis*, the male is blended with the female (probably through a kind of 'conjugation') by an actual continuity of tissue, immediately in front of her genital aperture, near the anterior third of the body.—Notwithstanding the simplicity of the structure of the ovarium, the number of ova produced by these Worms is very great; no fewer than 64 *millions* having been calculated to be contained at once in the single *Ascaris lumbricoides*, one of the commonest parasites of the Human intestine. In some of this order, the fertilized ova are retained within the body until they are hatched, so that the young come-forth alive; in other instances, the eggs are hatched subsequently to their deposition. In either case, however, the young worm at its emersion from the egg has the general form and aspect of its parent, though its structure is still far from being complete (Fig. 222, H); neither undergoing a metamorphosis, like the *Trematoda*, nor subsequently evolving the greater part of its structure by gradual development, like the *Cestoidea*.* Still it appears that certain Nematoid worms when developed in parenchymatous organs, may become encysted after the manner of the latter; and that, while they remain in this condition, their generative apparatus is undeveloped.

575. In the Generation of the *Rotifera*, many points remain to be elucidated. The female portion of the sexual apparatus is in general sufficiently conspicuous; consisting of an elongated ovarian mass, sometimes double, sometimes single, which is situated in the posterior part of the cavity of the body (of which it occupies a large portion, when the ova are near maturity), opening by a short oviduct into the cloacal cavity. The number of eggs in course of evolution at any one time, is always very small; but their size is considerable, in comparison with that of their parent. In regard to the male organs, however, there is much uncertainty. It has been shown by Mr. Dalrymple, that in a Rotifer of the genus *Notommata*, the sexes are distinct (the male, however, being entirely devoid of organs of nutrition, § 137), and that the fertilization of the ova is effected by an act of copulation; and there is reason to think that the like is true of some other genera. On the other hand, there is an absence of evidence as to the existence of separate males in many other genera; whilst in the bodies which contain ovaries, there are certain peculiar corpuscles, which may be considered as spermatozoa (as observed by Kölliker in *Megalotrocha*, and by Huxley in *Lacinularia*).†—The ova of Rotifera are sometimes incubated within the body of the female parent, so that the young comes-forth alive; are sometimes carried about by her, attached to the neighbourhood of the tail; and are sometimes freely deposited, and left to themselves.—The history of their embryonic

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* See Bagge "De Evolutione Strongyli et Ascaridis," 1841; Kölliker in "Müller's Archiv.," 1843; and Dr. Nelson 'On the Reproduction of *Ascaris Mystax*,' in "Philos. Transact." 1852.

† See Mr. Huxley's Memoir on *Lacinularia socialis*, in "Transact. of Microsc. Soc.," N. S., Vol. I., p. 1.

Development is in all essential respects the same as that of the Nematoid Entozoa; for the cells of the 'mulberry-mass' may be observed to arrange themselves into subordinate groups, each of which evolves some one of the principal organs; and thus the whole animal is completed, or nearly so, at the time of its emersion from the egg, nothing like a metamorphosis being observable, though the external appendages, and especially the rotatory organs, are still imperfect.* The whole process of development is completed, in some cases, within twenty-four hours; and hence, notwithstanding the small number of eggs which each individual produces at once, a most rapid multiplication takes place under favourable circumstances; it has been calculated by Prof. Ehrenberg that *seventeen millions* may thus be generated from a single parentage within twenty-four days.—Besides the ordinary ova thus rapidly developed and brought to maturity, many Rotifera produce what are termed 'winter eggs;' which have been commonly supposed to differ from the rest merely in possessing a peculiarly thick shell, which enables them to resist cold, and in being much longer in arriving at their full term, so as only to regenerate the species when the returning warmth of spring affords the conditions most favourable to their life. It is affirmed by Mr. Huxley (loc. cit. p. 14), however, that the production of these bodies is different from that of true ova; for whilst the latter are single cells which have undergone a special development, the former are aggregations of cells, in fact larger or smaller portions (sometimes the whole) of the ovary, being probably *gemmæ* which are evolved into zooids without fecundation, resembling the 'ephippial eggs' of *Daphnia* (§ 586), and those which give origin to the successive broods of *Aphides* (§ 580).

576. In the class of *Annelida*, we still find that Gemmation performs a very important part in the act of Reproduction: the multiplication of similar segments, which is so remarkable in many members of this group, being almost entirely due to it; while a spontaneous division sometimes takes place, by which the parts thus produced are detached from one another, sometimes in such a condition that they must be regarded as perfect zooids, whilst in other cases they seem but little more elevated in the scale of animality than are the detached oviferous segments of the Tænia. The complete reproduction by spontaneous fission may be seen to occur in *Nais*, a worm which, though aquatic in its habits, belongs to the order *Terricolæ;* after the number of segments in the body has been greatly multiplied by gemmation, a separation of those of the posterior portion begins to take place; a constriction forms itself about the beginning of the posterior third of the body, in front of which the alimentary canal undergoes a dilatation, whilst on the segment behind it, a proboscis and eyes are developed, so as to form the head of the young animal which is to be budded-off; and in due time, by the narrowing of the constriction, a complete separation is effected, and the young animal thenceforth leads an independent life. Not unfrequently, however, before its detachment, a new set of segments is developed in front of it, which is in like manner provided with a head, and separated from the main body by a partial constriction; and the same process may be repeated a second and even a third time; so that we may have in this

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* See Prof. Williamson 'On the Anatomy of *Melicerta ringens*,' in "Quarterly Microscopical Journal," Vol. I., p. 67.

animal the extraordinary phenomenon of four worms that are afterwards to exist as separate individuals, united end to end, receiving nourishment by one mouth, and possessing but one anal orifice. So long as this multiplication by gemmation is going-on, the proper generative apparatus remains undeveloped, as happens with the Hydra; but at a certain period of the year it ceases, the sexual organs are evolved, and eggs are produced and fertilized.—A parallel phenomenon has been observed in several genera of the *Dorsibranchiate* order; but the gemmæ thus detached are not truly-independent zooids, for each consists of little else than a generative apparatus, with the addition of locomotive organs; thus bearing a similar relation to their stock, with that which is borne by the generative segments of the Cestoid worms to the body from which they are budded-off (§ 570). In the one case, as in the other, it must be improper to reckon these segments as a new generation, since they are merely the 'complement' of the organism that would be incomplete without them. As many as six of these generative offsets have been seen in continuity with each other, and with their stock, by Prof. Milne-Edwards; the most posterior being evidently the oldest, and the one in direct connection with the parent consisting as yet but of a few segments, and being obviously the youngest.* A similar detachment of the generative segments has been observed among certain *Tubicolæ*.—There are several Annelida, which may be multiplied by artificial subdivision, each part being able to grow-up into the likeness of the perfect animal; though they do not spontaneously reproduce themselves in this mode.

577. The *Dorsibranchiate* Annelida, which were formerly supposed to be hermaphrodite and self-impregnating, are now known to be diœcious. The generative organs, whether male or female, are very commonly repeated in every segment of the trunk; and they form glandular masses, projecting between the muscular fasciculi into the general cavity of the body. Neither testes nor ovaria have any duct opening externally; but their products are discharged by rupture into the visceral cavity. In what manner they find their way out of this, or in what situation the ova are fertilized, is yet uncertain; but if, as there is some reason to believe, the fertilization is accomplished while the ova are still within the body of the female, this must be effected by the entrance of water through which the male spermatozoa have been diffused, into the visceral cavity. The females of some species carry their eggs about with them, after the escape of these from the interior of their bodies; the eggs being sometimes glued together by a mucous secretion, and sometimes protected within a kind of marsupial sac.—In the *Tubicolæ* also, it appears that the sexes are distinct; and as their peculiar mode of life does not allow the congress of two individuals, it is probable that the fertilization of the ova is effected by the diffusion of the seminal fluid through the surrounding water. This is, of course, much more likely to be effectual, owing to the gregarious habits of these animals.—Among the *Terricolæ*, whose organization is altogether higher than that of the proper Annelida, the generative organs, although both sexes are frequently combined in the same individual, are not multiplied to the same extent; for they are usually restricted to a small number of segments, and each set opens externally

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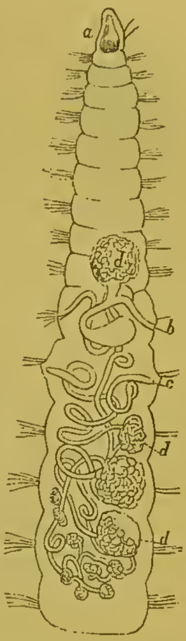
* "Ann. des Sci. Nat.," 3e Sér., Zool., Tom. III., p. 170.

by a single orifice; as is seen, for example, in the *Nais* (Fig. 253). They are not, however, self-impregnating; but a double congress takes place, as in the Planariæ, &c. In the *Earth-worm*, towards the end of the summer, there is developed around the body a thick and broad belt; this is an apparatus for suction, by which the worms are held-together during the congress. Here, too, the ova do not escape through the ducts which serve to convey the spermatic fluid to the ovaria; but the ovaria burst, when distended with mature ova, and allow their contents to be dispersed through the visceral cavity of the animal. In this respect the process of Generation in the earth-worm bears a striking analogy to that which we witness in Flowering-plants; for in the latter, the fertilizing influence is transmitted down the minute canals of the style, and the seeds escape, when ripe, by the dehiscence of the walls of their envelope. The ova of the earth-worm pass backwards between the integument and the intestine, to the anal extremity; and in their progress they gradually undergo their development, and are expelled from the parent, either as completely-formed worms, or surrounded by a dense and tough case, which gives them the character of pupæ. Whether they are produced in the perfect or in the pupal form, depends on the nature of the soil which the worms are inhabiting; in a light and loose soil, the young quit the parent prepared to act for themselves; but in a tough clayey soil, they continue the pupal form for some time, so as to arrive at a still higher degree of development, before commencing to maintain an independent existence. In many *Lumbricidæ*, as in the *Hirudinidæ* generally, the ova, after making their way outwards through the integument, gain a new investment from a secretion furnished by the cutaneous glandulæ of a particular part of the body, which sometimes forms a horny casing, sometimes a spongy envelope, of an annular form, closely fitting to the body. This is cast-off altogether by violent efforts on the part of the animal, the body being withdrawn from within it; and a sort of 'cocoon' is thus left, opening at both extremities, and usually containing from six to fourteen eggs, which undergo their development under its protection.

Fig. 253.

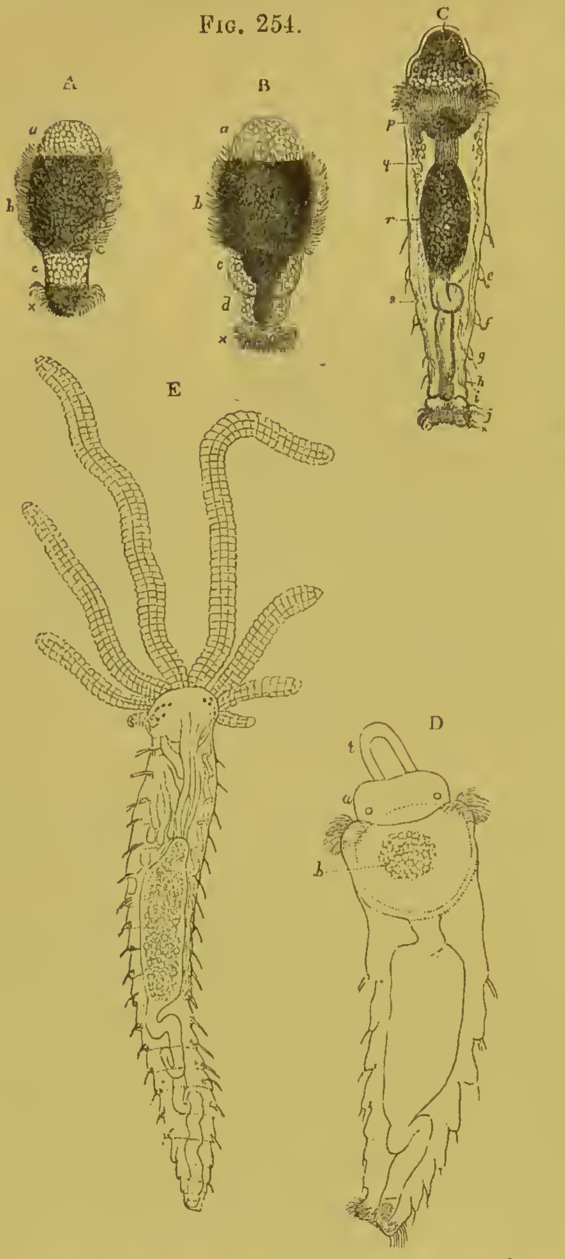


Generative Organs of *Nais filiformis*; *a*, head; *b*, aperture of male organs; *c*, aperture of female organs; *d*, *d*, ovaria.

578. In the history of the Development of the several orders of Annelida, there exists a very marked diversity; for whilst the young of the *Terricolæ* and *Suctoria* do not usually issue from the egg, until they have acquired the characteristic form of the parent (although the number of segments may be subsequently augmented), the embryoes of the *Dorsibranchiata* and *Tubicolæ* come-forth in a state of far less advancement, and only acquire their perfect form by such a series of changes as deserves the designation of a metamorphosis. So far as has been yet observed, there is a very close conformity in the earliest states of all these embryoes. They come-forth from the egg in a condition very little more advanced than the ciliated gemmules of the polypes; consisting of a nearly globular

mass of untransformed cells, certain parts of the surface of which are covered with cilia, symmetrically disposed. In the course of a few hours, however, this embryonic mass elongates, and indications of a segmental division become apparent; so that by the end of the first day after its emersion, there may be distinguished in the embryo of *Terebella* (Fig. 254, A) the cephalic segment, *a*, the first segment of the body, *b*, which is thickly covered with cilia, a second narrower and non-ciliated segment, *c*, and the caudal ciliated segment +. A little later (B), a new segment, *d*, is seen, interposed between the penultimate and the caudal segments; and the dark internal granular mass is observed to have extended itself to the extremity of the body, forming the first outline of the intestinal tube. The number of segments continues to increase by the process of gemmation, each new one being budded-off from the caudal extremity of the penultimate segment, so as to be interposed betwixt it and the original caudal segment, which is thus progressively removed from the cephalic, with which it was at first in close proximity. Thus in the larva in the more advanced stage represented at C, we find that the segments, *e*, *f*, *g*, *h*, *i*, *j*, have been interposed between the caudal segment + and the segment *d* of the previous growth (B); at the same time, the cephalic segment has become more developed, and the eye-spots are now very distinct; and each segment of the body is furnished with a pair of setigerous appendages, closely

FIG. 254.



Early stages of development of *Terebella nebulosa*; A, larva one day after its emersion from the egg;—B, larva more advanced, but still apodal;—C, further progress of the same, with first appearance of appendages; *a*, cephalic segment; *b*, ciliated segment; *c*, third ring; *d*, *e*, *f*, *g*, *h*, *i*, *j*, successively formed segments; × anal segment; *p*, pharynx; *q*, œsophagus; *r*, stomach; *s*, intestine:—D, larva at the end of the first period, showing the antenniform appendage, *t*, the cephalic segment, *a*, with its pair of ocelli, succeeded by the ciliated segment still bearing the remains of the collar of cilia, and containing the buccal cavity, *b*, in the interior of which ciliary movement may be discerned;—E, larva now become tubicolous, having eight antenniform appendages, multiple ocelli, more numerous segments, and more complete internal organization, but still having no special circulating apparatus.

resembling those of the adult. The evolution of the internal organs, also, has made considerable progress; so that we clearly distinguish the pharynx, *p*, the œsophagus, *q*, the stomach, *r*, (the walls of which are still tinged with the yolk-substance), and the intestine, *s*, as in process of formation. During this early period of their development, the embryoes remain in the midst of the gelatinous substance in which the ova were at first imbedded, and which appears to serve as the common 'albumen' for the whole collection; and from this substance they would seem to derive nutriment by imbibition, since they increase considerably in size before they become capable of receiving food through the mouth. It is only when the digestive apparatus and locomotive organs have attained a grade of development which enables the larvæ to obtain food for themselves, that they emerge from their gelatinous bed; and whatever may be their ultimate destination, they lead for a time a life of activity. When the communication is first established between the pharyngeal cavity and the external surface, so as to form the mouth, the interior of the passage, as well as the commencement of the intestinal canal, are lined with cilia; and it is by their agency that the young animal obtains its food, until other organs are developed. At this period (D, E), neither circulating apparatus nor distinct blood can be detected; nor can the presence of a nervous system be affirmed, although the existence of ocelli, and the activity of the movements of the larva, seem to justify the presumption that it is in process of formation.—The further development of the embryonic into the perfect form need not be traced in detail. It consists partly in the successive multiplication of segments, each new one being budded-off from the caudal extremity of the one that was formed last-before; and partly in the successive development of new organs, especially those constituting the circulatory, respiratory, nervo-muscular, and generative apparatus. In the *Tubicolæ*, the tubular envelope is usually formed after the larvæ have passed a few days in the condition of *Errantia;* and from that time the development of their locomotive apparatus takes a retrograde rather than an advancing direction.*

579. In the class *Myriapoda*, there is no known instance of multiplication by fission, either natural or artificial; and the act of reproduction is solely accomplished, therefore, through the Generative apparatus. The sexual organs are always diœcious, and the fertilization of the ova is accomplished by actual congress. The bodies of Myriapods present a considerable repetition of the generative, as well as of the other organs; but still there is by no means the same degree of segmental independence amongst them, as may be seen in the typical Annelida. The generative aperture, in both sexes, is near the anterior extremity of the body.—The history of the early development of the embryo within the egg, seems to correspond in its main features with that of Insects, which will be presently described; whilst in the later changes which are seen after its emersion, we are reminded of the Annelida; for the length of the body is greatly augmented by the successive addition of new segments, and these are formed by gemmation from the penultimate segment. It would seem as if the 'germinal capacity' were still expended (as in the lower classes) in the act of *growth* rather than of *development;* and as if the continued

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* See the admirable Memoir of Prof. Milne-Edwards 'Sur le Développement des Annélides,' in the "Ann. des Sei. Nat.," 3e Sér., Zool., Tom. III.

production of similar parts of a lower grade, were incompatible with the evolution of the previously-formed parts, into a higher type. We see, however, in the Myriapoda, that the advance of development is occasionally marked by the *aggregation* of segments that were originally distinct. This is especially the case in the *Scolopendridæ,* in which the multiplication of segments never takes place to anything like the same extent that it does in the *Iulidæ,* and in whose organisation there is obviously a greater approach to the concentration manifested in the higher Articulata. Thus the head, according to Mr. Newport, is composed of *eight* segments, which are often consolidated into one piece like the head of Insects; and each movable division of the body is in reality composed of two distinct segments, originally separate, but anchylosed together at an early period of their formation; their original distinctness being usually marked by the persistence of the separate ganglia and pairs of legs. The ganglia, however, sometimes coalesce, especially in the anterior part of the body of the *Polydesmidæ.*[*]

580. It is very remarkable that, in animals so highly organised as *Insects,* we should find a very marked example of Gemmiparous multiplication, occurring as part of the regular history of the race. This is the case in the genus *Aphis;* among many species of which, a large proportion of the individuals never acquire wings, but remain in the condition of larvæ (§ 584). These, without any sexual congress (none of them, indeed, having any male organs), bring forth, during the summer, living young ones resembling themselves; and the young soon repeat the same process in their turn, so that ten successional broods are often thus produced. With the fall of temperature at the end of the season, however, perfect winged males and females make their appearance; these copulate and produce true ova, which retain their vitality during the winter, and give birth to a new generation in the spring, long after the parents have perished. Now if we compare this series of phenomena with those of a similar kind which have already occupied our attention, it becomes obvious that although ova are evolved by the fertile larvæ, and although the development of these follows the same plan as that of the ova sexually produced and impregnated,[†] yet that this is really a case of *internal gemmation.* And thus, notwithstanding the great increase in the number of independent beings, and the long succession of broods of 'zooids,' which may be thus produced, not one of the viviparous larvæ becomes a complete organism; for so long as this method of multiplication is continuing, the type of the perfect insect is never evolved, since no true sexual characters make their appearance.[‡] So, again, the 'generation' cannot be said to be completed, until a perfect pair of male and female Aphides shall have been evolved, capable of continuing their race by the process of true sexual generation; and this evolution may be

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[*] See Mr. Newport's valuable Papers on the Myriapoda in the "Linnæan Transactions," Vol. XIX., and in the "Philosophical Transactions" for 1841, 1843, and 1844.

[†] See Leydig in "Siebold and Kölliker's Zeitschrift," 1850.

[‡] The viviparous pupæ are usually spoken of as 'females;' but they have no more real title to this designation, than is possessed by a Hydra which is budding-off new polypes from its body.—For a fuller and more controversial exposition of the Author's views on this subject, which are fully shared by Mr. Huxley, see the "Brit. and For. Med.-Chir. Rev." vol. iv., p. 443.

postponed for a much longer period than usual, by preventing the animals from being subjected to that depression of temperature, which, at the end of the warm season, ordinarily seems to check the gemmiparous multiplication, and to call into exercise the true sexual operation.*—Several other instances have been put on record, in which female insects which have been kept separate from males, have nevertheless produced fertile ova.—A remarkable case has lately been discovered by Prof. Filippi,† in which, in a parasitic larva resembling that of a Dipterous Insect, a vesicle makes its appearance, that gradually developes itself into the larval form of a Hymenopterous Insect; this internal gemma, for such it appears to be, gradually distends the larval body which preceded it, reducing it at last to a mere sac; and in due time, after passing into the pupa-state, it finally comes forth as a *Pteromalus*, one of the Ichneumon tribe. The uniformity of this curious occurrence seems to forbid its being regarded as a case of parasitism, which we might otherwise be disposed to consider it; and it can scarcely be ranked in any other category than that of *larval gemmation*.

581. All *perfect* Insects possess true Generative organs; and it is by them alone, that their reproduction is accomplished. Throughout the whole of this immense group, the sexual organs are constructed upon a plan essentially the same. They are invariably diœcious; and the outlet, both of the male and female organs, is situated at the posterior extremity of the body. The testes are always formed of cæcal tubuli, resembling those of glands in general; but there is such a variety in the mode in which these organs are disposed, that as many as twenty-four different types of them have been enumerated. The spermatic duct is often furnished with a vesicular dilatation, which serves as a reservoir for that fluid; and it terminates in a penis or intromittent organ, which is usually enclosed in a pair of valves prolonged from the last segment of the abdomen. The penis, or some neighbouring part, is frequently furnished with recurved hooks, that take a firm hold of the female during the act of coition. The ovaria of the female are formed upon very much the same plan as the testes; and present a similar variety in the arrangement of their parts. The number and degree of prolongation of their cæca, are usually in relation with the fertility of the species; and this is greatest in those Social Insects, in which a large proportion of the individuals never attain their full sexual perfection, the number of fertile females being very small. The development of the several parts of the ovum may be advantageously studied in this class; since the same ovarian cæcum very commonly contains ova in different stages of development. Here, as elsewhere (§ 526), the ovisac appears to be the part first formed, as the parent-cell of the ovum; this at first closely embraces the germinal vesicle, but soon a granular matter, the vitellus, is interposed between them; and when this has accumulated, a proper envelope, the vitelline membrane, is developed around it.—The females of many insects are provided with a *spermotheca*, or receptacle for the seminal fluid of the male; into this the fluid is received during coition; and there it is retained,

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* See "Burmeister's Entomology" (translated by Shuckhard) p. 310.

† See "Annals of Natural History," 2nd Ser., Vol. IX., p. 461.

without the loss of the vitality of the spermatozoa, for many weeks, so that each ovum is fertilized as it approaches the outlet. This outlet is frequently prolonged into an ovipositor; an instrument produced from the last segment of the abdomen (and apparently homologous with the sheath of the penis in the male), by which the ova may be conveyed into situations peculiarly appropriate for their reception. Special instruments are frequently developed in connection with the ovipositor, by which the parent is enabled to bore, or even to saw-out, a fitting receptacle; and the various provisions which are made in these and other ways, for the protection of the eggs and for the supply of food to the larvæ when hatched, are among the most curious manifestations of the *instincts* of this wonderful class.

582. The mode of Development of the Insect-larva within the egg, seems not very dissimilar to that which has been already described in the inferior Articulata. The entire yolk is divided by segmentation in the usual manner; but this subdivision takes place most minutely, and the formation of cells occurs most completely, at the peripheral portion; so that the first condition of the embryo within the egg, like that of the free-swimming embryo of Annelida, is a somewhat elongated body, composed of the vitelline mass included in a cellular envelope. This envelope, however, is first completed on that which is to become the *ventral* surface of the body; and on the dorsal aspect a broad open space is for some time left, through which the yolk may be clearly seen. This simple elongated body, however, soon exhibits a constriction, which marks-out the cephalic portion; and other segmental divisions early begin to show themselves, thus indicating the Articulated character of the animal, almost before its internal organisation can be said to have commenced. The dorsal opening is gradually closed; and the cellular membrane formed around the yolk presents a considerable increase in thickness, owing to the formation of new layers of cells. At the same time, the cells upon the surface of the included vitellus are undergoing subdivision and metamorphosis; and these form the walls of the alimentary canal, which thus includes the residue of the yolk. Various collections of cells are shortly seen, which are the respective foundations of the different organs that are to be developed in the larva; but the parts that usually first present an approach to the characters they present after the emersion of the embryo from the ovum, are those which, being concerned in mastication, are most directly subservient to that function which the larvæ exercise with such extraordinary energy, immediately on their entrance into the world. The mouth and anus are formed, as in other cases, by the thinning-away of the envelope which at first included the entire cavity; and not unfrequently the second of these orifices has not made its appearance, at the time of the escape of the larva from the egg.

583. No Insects come-forth from the egg in their perfect condition; and their state in many cases at the time of emersion is quite embryonic; so that it is usually not until a series of very considerable changes have taken place in external configuration and internal structure, together constituting what is known as the 'metamorphosis,' that the complete development of the specific type is attained. The amount of this metamorphosis, and the mode in which it is accomplished, vary considerably in the different orders of insects; but three stages are usually marked-out,

more or less distinctly, in the life of each individual. The term *Larva,* in the ordinary language of Entomology, is applied to the insect, from the date of its emersion from the egg, up to the time when the wings begin to appear; the term *Pupa* is in like manner employed to mark the period during which it is acquiring wings; and from the time when these and other organs characteristic of its perfect state are completed, it is spoken-of as the *Imago.* The grade of development, however, at which the Insect comes-forth from the egg, is very different in the several orders and families; and it is consequently very unphilosophical to associate under the same designation, beings which are in conditions essentially diverse. In all cases, the embryonic mass within the egg is first converted into a footless worm, resembling the higher Entozoa or the inferior Annelida in its general organisation, but possessing the number of segments—thirteen—which is typical of the class of Insects. Such, in the *Diptera* and *Hymenoptera,* and in some of the *Coleoptera,* is the condition of the larva at the time of its emersion from the egg; and it is remarkable that many of the larvæ of the first of these groups resemble Entozoa in their parasitic habits. The head, in larvæ of this kind (which are familiarly known as 'maggots'), differs but little from the segments of the body; the eyes in many instances not being developed, and the mouth being furnished with a mere suctorial disk. In the *Lepidoptera* and most of the *Coleoptera,* however, the larva at the time of its emersion possesses the rudiments of the three pairs of thoracic legs, although they are little else than simple claws (Fig. 255, 1, 2, 3), save in the carnivorous Beetles; whilst in addition to these, several of the abdominal segments are furnished with fleshy tubercles or pro-legs (generally to the number of four or five pairs), which are peculiar to the larva-state. In such larvæ (which are commonly designated as 'caterpillars'), we observe a remarkable equality in the different segments, both as to size, form, and plan of construction, which strongly reminds us of the Annelida. The alimentary canal occupies nearly the whole of the cavity of the body, and passes without flexure from one end of it to the other. The compartments of the dorsal vessel, the respiratory organs, the nervous centres, and the muscular bands, are repeated with great regularity; and there is as yet no distinction between the thoracic and abdominal portions of the trunk (Fig. 255). The head, however, is usually protected by a horny covering, and is provided with simple or clustered eyes like those of the higher Annelida and Myriapoda; and the mouth is furnished with powerful cutting jaws for the division of the food, which is usually vegetable in its nature. In the Orthopterous and Hemipterous orders, on the other hand, these stages of development are passed-through within the egg; and as the young Insect does not emerge thence until it has attained a higher grade, in which it presents a close resemblance to its parents in almost every particular save the want of wings, it cannot be regarded as having the characteristics of a real *larva.* This is the case, too, with some of the *Coleoptera,* in which order we find a considerable variety as regards the stage of development at which the embryo quits the ovum.—In the true Larva condition, the whole energy seems concentrated upon the nutritive functions; the quantity of food devoured is enormous; and the increase in the bulk of the body is very rapid. During this rapid growth, the caterpillar throws-off and renews its epidermis several times; but the larvæ of the Hymenoptera and Diptera do not undergo this exuviation until they pass into the pupa state, their integument being soft enough to yield to the distension from within. The sexual organs are but little developed during the larval period; but their rudiments may be detected. The activity of *growth*, however, seems to supersede in the larva the progress of *development;* for the tissues remain in an embryonic state, and the organs retain their original condition with little or no essential change except in size, until a sufficient store of nutriment has been taken into the system, to serve as the *pabulum* for all the subsequent developmental operations, by which the fabric of the perfect Insect is to be completed.

Fig. 255.

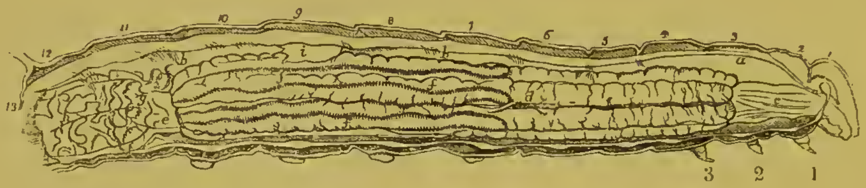
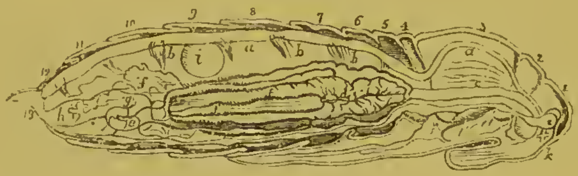


Fig. 256.



Ideal sections of Larva (Fig. 255) and Pupa (Fig. 256) of *Sphinx Ligustri* (Fig. 57), showing the relative state and position of their organs:—1-13, the successive segments; *a, a*, dorsal vessel; *b, b*, ligamentous bands holding it in its place; *c*, œsophagus; *d*, stomach; *e*, intestinal canal; *f*, biliary tubuli; *g*, cæcum; *h*, cloaca; *i*, sexual organ; *k*, cephalic ganglion, from which the ventral gangliated cord is seen passing backwards, along the floor of the thorax and abdomen.

584. Of the mode in which the Insect enters the *Pupa* state, and of its condition in that state, no general statement can be made; since they correspond for the most part with the grade of development, which the larva has previously attained. Where it already possesses the general form and structure of the Imago, and little else is required for its completion than the development of the wings and of the sexual organs, this is usually effected without any cessation of its activity; and after the first moult, which is regarded as marking the commencement of the pupa state, it continues to move about and to take food as usual, whilst its wings are sprouting and gradually becoming elongated beneath the next skin. This, again, is exuviated, and the wings as yet unexpanded are seen on the exterior of the body. After a third moult, the wings which were previously short, thick, and soft, are caused to expand, probably by the injection of air into their tracheæ; and no change subsequently takes place. Such is the case with the *Orthoptera, Hemiptera*, and some *Neuroptera*. It is curious to observe that in the viviparous broods of Aphides (§ 580), neither metamorphosis nor moulting takes place; but that the process of gemmation is performed in a condition, which corresponds with that of the larvæ of the perfect insects developed at the end of the season; as if the vital force which would otherwise be

directed to the complete evolution of the individual, is here employed in the multiplication of the race.—In the *Coleoptera, Lepidoptera, Hymenoptera, Diptera,* and some *Neuroptera,* however, the pupa-state is one of complete inactivity, as regards all the manifestations of *animal* life; although the formative processes are then carried-on with extraordinary energy. The imperfect larvæ of these orders, as we have already seen, are truly embryonic in their condition; and the processes of development which were commenced within the egg, and which were then only carried far enough to enable the larvæ to come-forth and obtain their own nutriment, are now continued at the expense of the food which they have collected and stored-up within their bodies; so that the passage into the pupa-state, in such cases, may be fairly likened to a re-entrance into the egg. The pupa is enclosed in the last skin exuviated by the larva, which, instead of being thrown-off, dries-up and remains to encase the proper skin of the pupa that is formed beneath it; and in addition to this, it is frequently protected by a silken 'cocoon,' the construction of which was the last act of larval life. The duration of the pupa-condition, and the rate at which the developmental changes take place, vary considerably in different cases; some Insects remaining in this state for years, whilst others pass through it in a few days or even in a few hours; in both cases, however, an important influence is exerted by external temperature. As the state of the Pupa is one of rapid transition, it cannot be said to have any characteristic organisation; the intermediate condition of its structure, however, between that of the Larva on the one hand, and that of the Imago on the other, is shown in Fig. 256.

585. The assumption of the *Imago* or perfect type of Insect-life, is always marked by an exuviation of the integument which covered the pupa; and with this are cast-off all the vestiges of the organs peculiar to the larva-state, while the wings, the true legs, the compound eyes, the antennæ, the complete masticating or suctorial apparatus, and many other organs, are now revealed for the first time in all those whose pupa-condition was inactive. The wings, however, are seldom ready for use at the time of the Insect's emersion from the pupa-case; being usually soft and moist, hanging loosely at the sides of the body, and only acquiring that rigidity which is requisite to give them the power of serving as organs of impulsion, when their tracheæ have been forcibly distended with air (§ 304). The nutritive apparatus of the Imago is far less developed relatively to the muscular, nervous, and sexual organs, than it is in the preceding conditions; and its subordination to the offices of these is shown by the fact, that many Insects take no food whatever after their last change, the sole purpose of their existence, in their perfect state, being the propagation of the race by the generative process. In many instances, the duration of the Imago-state is very brief, even where that of the preparatory periods has been very long; as in the case of the *Ephemera* (Day-fly), which usually dies within a few hours after its last change, although the term of its previous life as a larva and an active pupa has not been less than two or three years. And even where the length of the life of the perfect insect is much greater, as in Bees, Wasps, &c., it seems to have a special relation to the nurture of the offspring, which are tended and supplied with food during the whole

of their larva state. This duty, in the 'social' Insects, is performed by the 'neuters' or 'workers,' which are females whose sexual organs have not been evolved; their sexuality being proved (in the case of the Hive Bee at least) by the fact that they may be developed into perfect females by a different treatment during the larva-state (§ 119). In the *Ant* tribe, the neuters do not acquire wings; and some of them, which are two or three times the size of the rest, and are somewhat differently formed, are characterized as 'soldiers,' their special office being the defence of the nest rather than the nurture of the young. Among the *Termites* (White-ants), however, the 'soldiers' appear to be *pupæ* arrested in their development; whilst the 'workers' have the characters of permanent *larvæ.*—In the *Apterous* orders of Insects, we find some tribes undergoing a regular metamorphosis, which is complete in every respect save the non-development of the wings. Thus the larvæ of the *Pulex* (Flea) are footless worms, which afterwards pass into the pupa-state, spinning for themselves a silken cocoon; in this they remain inactive for about twelve days, after which the imago comes forth, having the rudiments of wings attached to the second and third segments of the body, though without any proper distinction of thorax and abdomen. The *Pediculus* (Louse), *Podura* (Spring-tail), and some other Aptera, however, undergo no metamorphosis; coming-forth from the egg in the condition in which they remain all their lives; and this being far from the type of the perfect Insect.

586. Although in the higher *Crustacea,* as in Insects generally, the power of multiplication by Gemmation seems entirely wanting; yet in the Entomostracous group we have instances of it, which seem to correspond in their essential features with the case of the Aphis (§ 580). For whilst, in *Daphnia,* the true sexual Generation takes place at certain seasons only (the males disappearing entirely at other times), a non-sexual production continues at all periods of the year, so long as warmth and food are supplied, and is repeated by each of the successive broods thus evolved; and the same appears to be the case with *Cypris,* the male of which, however, has not yet been discovered. It seems probable, moreover, that the production of 'ephippial eggs,' which is a very peculiar feature in the physiological history of *Daphnia,* is to be considered as a case of 'larval gemmation.' For the first trace of the 'ephippium' presents itself after the third moult, as a collection of green matter in the ovaries, which differs from a mass of ova both in colour and in appearance; this, after the fourth moult, passes from the ovaries into the 'matrix,' an open space between the back of the animal and its carapace; and there becomes developed into the 'ephippium,' which is a mass of hexagonal cells of dense texture, that encloses two oval bodies, each consisting of an ovum covered with a horny casing, enveloped in a capsule which opens like a bivalve shell. The 'ephippium' is thrown-off at the fifth moult, and floats on the water until the next year, when the young are hatched with the returning warmth of spring. This curious provision seems destined to afford protection to the eggs which are to endure the severity of winter cold; and it is obviously analogous to that production of 'winter eggs' among the Rotifera, which, as already pointed-out, probably results from an act of gemmation, not from sexual generation. It has been ascertained by Dr. Baird, that the young pro-

duced from the ephippial eggs, and kept in seclusion from each other, have the same power of continuing the race by non-sexual reproduction, as is possessed by those developed from ordinary ova.*—Although no propagation by spontaneous fission or gemmation is known to take place among the higher Crustacea, yet they retain a power of regenerating lost parts which is truly astonishing, the complexity of their organization being considered. This extends to all the members, and seems essentially connected with the moulting process; the new limbs making their first appearance when the shell has been cast-off, and becoming more and more like those which had been lost, with each successive exuviation.†

587. Although it seems probable that the *Entomostraca* are diœcious like the higher Crustacea, yet the male of many species has not been discovered; probably on account of its dissimilarity to the female in size and aspect, and from making its appearance only during a very limited period; as is the case with many of which the males *are* known, having been seen in actual congress with the females. A single act of copulation serves to impregnate, not merely the ova which are then mature or nearly so, but all those subsequently produced by the same female, although they may be matured at considerable intervals. The eggs of some Entomostraca are deposited freely in the water, or are carefully attached to clusters of aquatic plants; but they are more frequently carried by the parent in special pouches, developed from the posterior part of the body by an extension of the membrane covering the proper ovaries (Figs. 60, B, 75, B, *b b*); and in many cases they are retained there until the young are ready to come-forth, so that these animals may be said to be ovoviviparous. In the *Daphnia,* the eggs are received into a large cavity between the back of the animal and its shell; and there the young undergo almost their whole development, so as to come-forth in a form nearly resembling that of their parent. But in most Entomostraca, the young come-forth from the egg, at once into the world, in a condition that differs essentially from that of their parent; especially in having only the thoracic portion of the body as yet evolved, and in possessing but a small number of locomotive appendages; the visual organs, too, being frequently wanting at first (Fig. 60, C—G). The process of development, however, takes place with great rapidity; the animal at each successive moult (which process is very commonly repeated at intervals of a day or two) presenting some new parts, and becoming more and more like its parent. In the case of the parasitic suctorial Entomostraca, the change of form, at least in the female, is often very remarkable; but it is occasioned for the most part, by the development of the prehensile apparatus by which the parasite attaches itself to the seat it has selected, and by the enormous enlargement of the ovaries and egg-sacs, which often assume very strange forms (Fig. 75, C—F).—The early development of the ovum has yet been only imperfectly studied; but it would seem as if the whole mass of the yolk-cells formed by segmentation, goes at once to transform itself into the embryonic structure, as in the lower Articulata.‡

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[*] "Natural History of British Entomostraca," published by the Ray Society, pp. 79, 80.

[†] For a number of curious examples of this phenomenon, see Sir J. G. Dalyell's "Powers of the Creator displayed in the Creation," Vol. I., pp. 169, *et seq.*

[‡] See Prof. Van Beneden 'Sur le Développement des Nicothoés,' in "Ann. des Sci. Nat.," 3e Sér., Zool., Tom. XIII.

588. The sexes are undoubtedly distinct among all the higher Crustacea; and the fertilization of the ova is effected by an act of copulation, whilst they are yet within the body of the female. The Generative apparatus, in the one sex as in the other, presents this remarkable difference from that of Insects, that the two lateral halves of it do not unite on the median line so as to have a common outlet; but that the external orifices of the seminal organs and of the ovaries are separate on the two sides. This independence of the lateral halves of the sexual apparatus appears to have some relation with the frequency of 'lateral hermaphrodism' in this class; monstrosities being of no unusual occurrence, in which the male character is exhibited by the sexual organs of one side, and the female by those of the other. A progressive complication in the structure of the generative apparatus presents itself, as we ascend from the lower to the higher forms of this division of the Crustacea; for whilst in the inferior tribes the testes consist of a small number of vesicles opening into a common tube on either side, each is made-up in the higher of a mass of minute convoluted tubes (Fig. 58, *f*), opening into a common duct, which is often dilated into a receptacle for the seminal secretion; and the ovaria, also, which are but a pair of simple sacculi in the inferior tribes, show a division in the superior into the proper ovaries (which are long branching cæca communicating with each other on the two sides), the oviducts, and the *spermothecæ* or copulatory pouches. The orifices of the male organs are usually stated to be in the first joints of the last pair of thoracic limbs; and it has been supposed that the first and second pairs of abdominal appendages, or false legs, serve as exciting organs. From the observations of Mr. Spence Bate,* however, it appears that the spermatic duct of each side passes-on as a membranous tube from the base of the thoracic duct to the first or second abdominal appendage, and runs to the extremity of this, which thus, as it is introduced into the female canals, becomes a true penis or intromittent organ. The spermatic fluid, received and stored-up in the spermotheca whilst it is itself immature (§ 521), may remain there for a considerable time, and may fertilize ova which are far from being completely developed at the time of copulation. The fertilized ova, after their extrusion from the oviduct, are usually carried-about by the female parent, supported either by the thoracic or by the abdominal appendages, until the embryo is nearly ready to come-forth; and special provisions for their protection are afforded, in many Crustacea, by the peculiar development of these appendages.

589. The early stages of embryonic Development in the Crustacea have not yet been fully made-out. It would seem as if, in the *Decapods* (as in the Arachnida), the germinal membrane springs from a spot on one side, instead of arising, as in Insects, out of the peripheral portion of the 'mulberry mass' by the more minute subdivision of its cells. However, it gradually extends itself round the yolk, the dorsal region, as in Insects, being the last to close-in; and whilst it is yet but a disk on one side of the yolk, it exhibits a distinct separation between the cephalic portion and the trunk, other indications of segmental division making themselves apparent as the development proceeds. Here, too, as in Insects, the parts about the mouth are the first to attain some degree of completement. The relation which the young Crustacean, at the time of its

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* "Ann. of Nat. Hist.," 2nd Ser., Vol. VI., p. 109.

emersion from the egg, bears to the adult, seems to differ greatly in different tribes, and even in genera which are closely allied; some, as the *Astacus fluviatilis* (cray-fish) and the *Gecarcinus* (land-crab), coming-forth in a form which corresponds in all essential particulars with that of the parent; whilst in others, as the *Astacus marinus* (lobster), *Palinurus* (rock-lobster), *Palemon* (prawn), *Crangon* (shrimp), and *Carcinus mœnas* (common crab), the form of the young at the time of its emersion differs greatly from that of the parent, which is only acquired after such a series of changes as constitutes a true metamorphosis. In most of the latter cases, besides other alterations, an increase (which is sometimes very considerable) takes place in the number of segments; it is not due, however, as in Annelida and Myriapoda, to the repeated subdivision of the terminal or penultimate segment only; for the last segment of each of the three great divisions of the body, the head, the thorax, and the abdomen, seems to possess the gemmiparous power, so that the number of segments in each of these regions is separately augmented. Generally speaking, a strong resemblance exists among the young of all the species which undergo a metamorphosis; the head and thorax being included within a large carapace (Fig. 77, A), while the abdominal portion is so much developed as to make up the chief part of the length of the body; and the thoracic segments being furnished with 'fin-feet,' whilst the abdominal segments are destitute of appendages, the last, however, being flattened-out into a large tail-fin. In this condition, they bear so strong a resemblance to some forms of Entomostraca, as to have been actually mistaken for members of that group. In the *Macrourous* Decapods (lobster, prawn, &c.), the metamorphosis chiefly consists in the replacement of the thoracic fin-feet by true locomotive appendages and by a special apparatus of respiration (§ 294), and in the development of abdominal appendages and of peduncles to the eyes. But in the *Brachyoura* (Crabs, &c.), a much more complete change takes place; the thorax being gradually developed at the expense of the abdomen, which becomes rudimentary; the swimming members being replaced by limbs fitted only for walking, whilst those of the anterior pair are developed into large *chelæ* or claws (Fig. 77, B, C, D); and a special respiratory apparatus being developed beneath the carapace, the eyes also becoming pedunculated, as in Macroura.*

590. The mode in which the generative operation is performed in the group of *Cirrhipeds*, the real rank of which seems to be that of a sub-class of Crustacea (§ 14), presents, according to the recent researches of Mr. C. Darwin, some extremely curious phenomena.† In most of the species of this group, each individual possesses both kinds of sexual organs, and appears to be self-fertilizing. The testes, which are small and leaden-coloured, lie in apposition with the stomach, sometimes entering the basal segments of the members, and extending (in the pedunculated division of the group) into the pedicles; their ducts are furnished with a pair of large vesiculæ seminales; and from these proceed two canals, which, uniting

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* The Metamorphosis of Crustacea was first brought to light by Mr. V. Thompson, "Zoological Researches," Part I., and "Philos. Transact.," 1835; his observations have been confirmed by Ducane, Rathké, Goodsir, and R. Couch; an admirable summary of whose investigations is contained in the Introduction to Prof. T. Bell's "History of the British Stalk-Eyed Crustacea."

† See his "Monograph on the Sub-Class *Cirripedia*," published by the Ray Society, and the Art. 'Cirripedia' in the "English Cyclopædia."

into a single tube, convey the fluid to a proboscidiform penis (Fig. 5, *g*) often of considerable length, and articulated like the cirrhi. The female genital organs are far more massive, occupying, in the pedunculated division, a great part of the cavity of the pedicle with branching tubes, as well as forming a pair of large compact glandular masses in the body itself; the relative functions of these two parts are not certainly known, but it seems not unlikely that (as in many Entozoa) the former may supply the vitelline cells, and the latter the germinal vesicles. The ova of the *Lepadidæ*, when mature, burst-forth from the ovarian tubes in the peduncle and round the 'sack' (or mantle-like investment of the body); and, by some means yet imperfectly understood, become aggregated into two lamellar masses, that enfold the body almost like the valves of a bivalve shell, and are attached to it by a fold of skin on each side. These lamellæ remind us of the egg-sacs of the *Rotifera* and *Entomostraca* (Figs. 60, 75); the investment of the ova, however, seems to be formed, not as in these groups by a projection of the membrane of the proper ovaries, but by an extension of the corium between the old outer integument which is about to be exuviated, and the new chitine tunic formed within. The ova are probably impregnated after their escape from the ovaries, when they first find their way into the 'sack,' and whilst the membrane of the lamellæ is yet tender; and they remain in the lamellæ until the embryoes are fit to come-forth. A general account of the subsequent phases of their development (the early stages of which are passed-through within the 'sack' of the parent) has already been given (§ 14).

591. Although hermaphrodism is the general rule in this group, yet there are exceptions to this; for in certain species of *Ibla*, *Scalpellum*, *Alcippe*, and *Cryptophialus*, the sexes are separate, and the males (as in many Entomostraca) are very inferior in size, and even (as in some Rotifera) extremely imperfect in organisation. In *Ibla*, the male is attached to the 'sack' of the female; it has a well-organized mouth supported on a peduncle, but has no more than a rudiment of the thorax, and only two pairs of aborted cirrhi. In some species of *Scalpellum*, the males, though small, and attached within the valves of the female, have the ordinary structure of pedunculated Cirrhipeds; but in other species they are far less completely developed, consisting merely of a sac, with rudiments of four valves, inclosing a singularly-modified thorax, with only four pairs of appendages which cannot be called cirrhi, and being destitute of mouth and stomach. The males of *Cryptophialus* and *Alcippe* are even more rudimentary; for they are reduced to an outer envelope, a single eye, testes, vesicula seminalis, and a wonderfully-elongated proboscidiform male organ; there being neither mouth, stomach, thorax, abdomen, nor cirrhi. It may be doubted whether there exist in the whole animal kingdom, any creatures in a more rudimentary condition than these males. As they do not possess a mouth or stomach, they are necessarily short-lived. The pupa fixes itself on the female, becomes cemented to her, undergoes its last metamorphosis, and becomes a male Cirrhipede; the spermatozoa are matured and discharged; the male dies, decays, and generally drops-off; and it is succeeded, when the ova in the female are next ready for impregnation, by one or more fresh males. Owing apparently to the small size of the males, there is usually more than one attached to the female at the same time; and in the case of *Alcippe lampas*,

Mr. Darwin found no less than thirteen of these singular parasitic and rudimentary males attached to a single female.—It is still more singular, however, that in the *hermaphrodite* species of *Ibla* and *Scalpellum*, there should be found *males* resembling those of the unisexual species, and attached in a similar manner. These are termed by Mr. Darwin 'complemental males,' inasmuch as they seem complementary in function to the male organs of the hermaphrodite. Although we have no known parallel case in the Animal Kingdom, yet the Vegetable world furnishes many analogous instances; it not being at all uncommon, especially among the *Compositæ*, to find male flowers (often in a rudimentary condition, like the 'complemental males' of Cirrhipeds) superadded to perfect hermaphrodite flowers. Within the limits of the two genera just named, therefore, we have the following singular varieties:—1st, a female, with a male (or rarely two) permanently attached to her, protected by her, and nourished by any minute animals that may enter her sac: (2nd) a female, with successive pairs of short-lived males, destitute of mouth and stomach, inhabiting two pouches formed on the under-sides of her valves; (3rd) a hermaphrodite with a male (occasionally two or three) attached to the interior of the valves, and capable of seizing and devouring prey in the ordinary Cirrhipedal method: and (4th), a hermaphrodite, with from one or two, up to five or six, short-lived males, without mouth or stomach, attached to one particular spot on each side of the orifice of the capitulum.*

592. In the class *Arachnida*, there does not exist, so far as is yet known, any example of Gemmiparous reproduction; though looking to the very low grade of development of some of the *Acaridæ* (mites, &c.), and the embryonic condition in which some of their organs and tissues remain, it would not seem improbable that the same mode of multiplication may present itself among them, as we have seen to exist in the Aphides and in certain Entomostracous Crustacea. This expectation may seem to be justified by the large amount of regenerative power (another manifestation of the same 'germinal capacity'), which exists even in the highest Arachnida; for this extends, as in the Crustacea, to the reproduction of entire limbs.—The sexes are separated in all but the lowest members of this class; and the ova are fertilized by a complete congress, which is accomplished among the *Araneidæ* in a very curious manner. The spermatic organs of the male Spider are two long worm-like tubes, which commence at the posterior end of the abdomen, either by a simple cæcal termination, or by an oblong vesicle; and which terminate, either by a single or double orifice, on a slit in the integument of the under side of the abdomen, near its anterior extremity, in a

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* "As I am summing-up," says Mr. Darwin (Op. cit., p. 293), "the singularity of the phenomena here presented, I will allude to the marvellous assemblage of beings seen by me within the sack of an *Ibla quadrivalvis*;—namely, an old and young male, both minute, worm-like, destitute of a capitulum, with a great mouth, and rudimentary thorax and limbs, attached to each other and to the hermaphrodite, which latter is utterly different in appearance and structure; secondly, the four or five free boat-shaped larvæ, with their curious prehensile antennæ, two great compound eyes, no mouth, and six natatory legs; and lastly, several hundreds of the larvæ in their first stage of development, globular, with horn-shaped projections on their carapaces, minute single eyes, filiform antennæ, probosciformed mouths, and only three pair of natatory legs;—what diverse beings, with scarcely anything in common, and yet all belonging to the same species."

position corresponding to that of the vulva of the female. The palpi, however, contain the organs by which the spermatic fluid is introduced; each of these being furnished with a tubular projection, terminated by a horny appendage, which, when not in use, is retracted within the last joint of the palp. No connection whatever can be traced between the organs which prepare the spermatic fluid, and these intromittent instruments; nevertheless it has been ascertained by repeated observations, that no closer sexual congress takes place, than the introduction of these appendages of the palpi within the vulva of the female; and it would seem probable that the male himself applies these appendages to his abdominal aperture, and charges them with the fertilizing fluid, before the act of intromission. The ovarium of the female Spider is a simple elongated vesicle, closed at one extremity, and communicating at the other with a slender oviduct, that terminates at the corresponding side of the transverse fissure, which, as in the male, is situated between the anterior pulmonic cavities; when this ovarium is dilated with ova, it occupies a considerable part of the abdominal cavity. The peculiar mode of sexual congress just described, seems to have relation to the remarkable instinct which prompts the female spider to attack and devour the male, as soon as the fertilization of her ova is accomplished; which her superior size and strength enable her to do, if he remain within her reach. It is obvious that if the orifice of his sexual canal were applied to hers, his danger would be augmented with this closer approximation. It is curious that, with such an instinct towards the opposite sex, the attachment displayed by the female towards her offspring should be of most extraordinary strength. The ova are generally enveloped in a soft and warm silken cocoon, which she guards with the most jealous care. Some species carry this about with them; others attach it to trees, or hide it in empty snail-shells. Within this the young remain until their development is completed, and they then make their way out. The mother generally foregoes all nourishment during her watch; and if the young are prevented by the coldness of the weather from coming-forth at the accustomed time, she will die of hunger rather than quit her post.—In the *Scorpionidæ*, the testes and ovaria are formed upon the same general plan as in the Araneidæ, but are more complex in their structure; the outlet by which they terminate is situated at the middle of the under side of the last segment of the thorax; and as the palpi are destitute of the peculiar appendages which they possess in the Spiders, it is probable that they do not take any share in the sexual operation. The ova are retained in a dilatation of the oviduct, until the young are mature; so that the egg-case is ruptured within the body of the parent, and the young are born alive.—There seems reason to believe that in some, at least, of the *Acaridæ*, the sexes are united; and in the larger proportion of this order, there appears to be no definite ovarium, the ova being lodged in the general substance of the tissues.

593. The history of the embryonic Development of the *Arachnida* has hitherto been chiefly studied in the Spider; and the observations of Herold * upon this point, valuable as they are, leave much to be elucidated in the early history of the process. The vitelline sac is invested

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* "De Generatione Aranearum in Ovo," 1824; also, for the *Scorpionidæ*, Kölliker in "Muller's Archiv.," 1843.

in an outer tegument, or chorion; and between the two is a layer of albumen, as in the Fowl's egg. The vitellus, as in the ovum of Cephalopods, Fishes, and Birds, consists of two parts, the 'germ-yolk,' and the 'food-yolk;' and it is the former alone, which undergoes the process of cleavage. A *cicatricula*, or 'germ-spot,' is thus formed on one side of the principal mass of the yolk; and from this a cellulo-membranous expansion takes place, which gradually invests the whole vitellus; the part which is to become the dorsal region of the animal, being, as in other Articulata, the last to close-in. A thickening of this 'germinal membrane' takes place in the seat of the original germ-spot; and it is here that the foundation is laid for the development of the principal organs. In the first place, the part which is to become the cephalic segment is separated by a constriction from the principal mass; the four segments of the thorax are indicated by parallel fissures on either side; and the abdominal portion is marked-off by a deeper constriction. The rudiments of the principal appendages to the head soon begin to bud forth from the cephalic segment; and the characteristic group of simple eyes early shows itself. The rudiments of the thoracic members soon appear, budding-forth from their respective segments; and the simple alimentary canal is formed around the vitelline mass, at first wide, but gradually contracting, as the material of the yolk is appropriated to the formation of the tissues. The mouth and anus, as in other cases, do not make their appearance until a later period; but even up to this time, although the posterior part of the dorsal vessel is seen along the upper curvature of the abdomen, the integument has not completely closed-in over the dorsal portion of the thorax. This closure, however, gradually takes place; the cephalic and thoracic members are perfected; the development of the internal organs advances in a corresponding degree; and the young Spider comes-forth from the egg in a form and condition which differ very little from that of its parent, whose size it gradually attains by simple *growth*.—Thus the whole *nisus* of development in the Spider appears to be directed, even from the earliest period, to the evolution of the complete organism; and no part can be said to be evolved for a mere temporary purpose, the entire germinal membrane remaining persistent as the integument of the Animal.—Among the *Acaridæ*, the ova are generally deposited and left to themselves, the young coming-forth in due time in a form resembling that of their parents, except that they have only six legs instead of eight, the deficient pair being supplied at the first moult.

594. In no animal belonging to the *Vertebrated* series, do we ever witness the least approach, after its characteristic form has been attained, to the production of a distinct individual by Gemmation; but, as already stated (§ 475), a partial separation may take place in the germinal mass at an early period of its development, which may give rise to the subsequent evolution of supernumerary parts, or even to the duplication of the entire structure. This mode of explaining the phenomena of 'monstrosity by excess' is the only one that can be applied with the least show of probability to cases of 'monstrosity by inclusion.' In these last, organs and tissues that seem like fragments of a fœtal body, are found imbedded in the midst of another organism; and this not merely in the bodies of females, in which their presence might be attributed to the abnormal

development of the normal generative products; but in those of males, in which no such origin could be assigned to them, and in which gemmation at an early period of embryonic life seems the only admissible alternative. —The only indication of the persistence of this 'germinal capacity' in the organism which has once attained the Vertebrated type, is that which is exhibited in the restoration or reparation of lost or injured parts; and on this point there is nothing to add to what has been already stated (§ 475).

595. The type of the true Generative apparatus in the class of *Fishes*, presents little elevation above that which it possesses in the higher Invertebrata. For both the testes and ovaria of the greater number of Osseous Fishes seem to be constructed upon the same plan with those of the Cephalopoda; each of these organs having a common cavity into which their products are received, and from which they are directly conveyed to the outlet by an efferent duct. In all the Cartilaginous Fishes, however, and in a few of the Osseous, the arrangement resembles that which prevails among the higher Vertebrata; for the ovary is unprovided with an excretory duct, and the ova, when set-free from it, fall into the cavity of the abdomen. In the Cyclostome fishes, they find their way out of this cavity by a simple orifice situated behind the anus; an arrangement that reminds us of that which exists in the Earth-worm. In the Sharks and Rays, on the other hand, the margin of the orifice is prolonged inwards, so as to form a sort of funnel, into which the ova are received when they escape from the ovary, and which conveys them towards the outlet; an arrangement that obviously foreshadows the genital canal and the Fallopian tubes of Mammalia.—In the *Osseous Fishes* generally, there is no sexual congress; but the ova discharged by the female are fertilized by the seminal fluid diffused through the water of the neighbourhood by the male. In the case of the Stickleback and a few other fishes, however, which construct nests, it appears that when the ova have been deposited in these, the male discharges his seminal fluid upon them. Of the ova for whose fertilization no such special provision exists, a large proportion are likely to be unproductive; and of the young actually hatched, the greater number soon perish for want of protection by their parents, falling a prey to the voracity of other fishes. Hence arises the necessity for the enormous fecundity of these animals, and for the size of their generative organs. It has been calculated that above a million of eggs are produced at once by a single Cod; and in other species the amount may be still greater. A very curious fact in the history of the generative system of Fishes, is that the male is frequently capable of the reproductive act, when far from his own full growth. Several mistakes have arisen from this source; the young with fully-developed milts having been mistaken for adults; and having been described as distinct species, on account of the difference of their size and markings, both of which subsequently undergo a change. Thus the fish commonly known as the Parr, is actually the young of the Salmon in the second year.—Among the *Cartilaginous Fishes*, on the other hand, the fertilization of the ova is usually effected whilst they are yet within the oviducts, by an actual congress of the sexes; and there are several of these, in which the embryo undergoes nearly its entire development within the body of the parent, so that the young are produced alive. In some species of Ray

and Shark, the oviduct is found to have a sort of uterine enlargement near its termination, in which the ova are delayed for some time, and in which they receive a degree of additional assistance from the parent, which foreshadows the more complex provision for this object in Mammalia. There is no *direct* communication between the blood-vessels of the parent and those of the fœtus; but the membranes of the latter absorb nutriment from the extremely vascular lining of the oviduct of the former, to such an extent that, in the *Torpedo*, the weight of the mature fœtus is between two and three times that of the egg.* The ova of the higher Cartilaginous fishes, in which their fertilization is secured by sexual congress, and in which a provision of some kind exists for their protection during the period of embryonic development, are much fewer in number than those of the Osseous.—One of the most curious provisions for the early protection of the offspring in this class, is that which we find in the *Syngnathidæ* or Pipe-fishes. The *male*, in most of these, has a pouch on the under side of its body, formed by the meeting of two folds of skin; into this, the eggs deposited by the female are conveyed; and here they remain, until the young attain a considerable degree of development. Even when able to swim about by themselves, they seek the protection afforded by this curious contrivance; which closely resembles that with which we are familiar in the Marsupial Mammalia, differing from it, nevertheless, in the absence of any special means of affording nutrition to the embryo. In some species of this group, however, the pouch is absent; but the ova are received into a set of hemispherical depressions on the under side of the abdomen, to which they attach themselves by their gelatinous envelope. The *Gobius niger* constructs a regular nest among sea-weeds, in which it deposits its ova; and these it watches with maternal care until they are hatched. A very elaborate nest is constructed by the male of the fresh-water *Stickleback*; and it is carefully watched by him during the period of embryonic development, in order to guard the eggs from the voracity of the females, who are continually endeavouring to make a prey of its contents.

596. In *Reptiles*, we find the Generative apparatus exhibiting a manifest advance, in degree of organization, from the highest form in which it exists in Fishes; and the fertilization of the ova is not left to the chance-contact of the seminal fluid that may have been dispersed through the neighbouring water, but is either accomplished before they have been expelled from the female passages, by the introduction of the seminal fluid within these, or in the very act of expulsion. The latter is the case in the Frog and its allies; the former, in most of the higher Reptiles, many of which possess a penis or intromittent organ. The 'testes' or spermatic organs of Frogs shew an approach to the structure which is characteristic of higher Vertebrata, being composed of an aggregation of numerous short cæca, the representatives of the tubuli seminiferi; but they discharge their secretion by several excretory ducts, which open into the ureters, instead of uniting into a distinct spermatic canal or 'vas deferens.' The ovaries of the female are composed of

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* In these animals, the temporary branchial filaments are extremely long, and appear to serve as special absorbing organs; in Dr. Davy's opinion, their function is particularly subservient to the development of the electrical apparatus. See his "Anatomical and Physiological Researches," Vol. I., p. 67.

duplicatures of a vascular membrane in which the ova are developed, and these lie in the posterior or pelvic portion of the visceral cavity; but, on the other hand, the oviducts are prolonged forwards nearly as far as the heart, and there terminate by open fimbriated extremities; the ova, therefore, set-free in the abdominal cavity by dehiscence from the surface of the ovary, must travel from the posterior towards the anterior extremity of the visceral cavity, before they can enter the dilated orifice of the oviduct which is to convey them forth.—In the higher Reptiles, the testes exhibit a decided advance in development, in the greater length and convolution, and in the diminished multiplication, of the tubuli seminiferi; and the products of each testis are collected into a single excretory duct or 'vas deferens,' which does not open into the ureter, but either discharges the spermatic fluid into the cloaca, or is continued as a groove along the penis, and conveys the fluid to its extremity. The internal orifices of the oviducts in the female approach more closely to the ovaries; and these organs present a more compact structure. The oviducts invariably open externally into the cloaca, and the ova are usually discharged soon after fertilization, if not before. In Batrachia, Ophidia, and Sauria, however, there are certain species which retain their ova in a sort of uterine cavity formed by a dilatation of the oviduct near its extremity, until the development of their contained embryo is so far advanced, that the enveloping membrane ruptures in the very act of the expulsion of the ovum, or even previously, so that the young are born alive. This is normally the case, for example, with the Land Salamander, and frequently also with the Viper, Slow-worm, and common Lizard; the egg being retained until the embryo has attained its full development, and the enveloping membrane being usually burst (as Mr. Bell* considers) in the act of parturition. With these animals, as indeed with all Reptiles, a high degree of heat is necessary for the maturation of the eggs; a portion of this heat seems to be developed within the body of the parent herself, by some peculiar excitement of the calorifying power which these animals possess (§ 444); but the gravid female may often be seen basking in the sun, acquiring from its rays the caloric which she is not herself capable of generating.—In the oviparous Reptiles, it is not common to find the parent affording any protection to the eggs when once deposited, or to the young produced from them. The *Pipa Americana* (Surinam Toad), however, is an exception; in this species, the female has on her back a number of cells hollowed in the integument; in these the eggs are placed by the male, when she has deposited them; and here they remain for about 80 days, during which time the embryoes undergo their metamorphosis, so as to come forth as perfect Frogs. It has been satisfactorily determined that the gelatinous mass in which the ova of Frogs are imbedded, serves for the first nutriment of the young Tadpoles on their emergence from the egg; and the same is probably the case in many other instances.

597. In *Birds*, the generative apparatus does not manifest any great advance beyond the form it presents in Reptiles; but there is always a provision for the fertilization of the ova, by sexual congress, soon after they have been discharged from the ovaria. The 'testes' or spermatic organs of the male, are compact bodies of a globular or elongated form,

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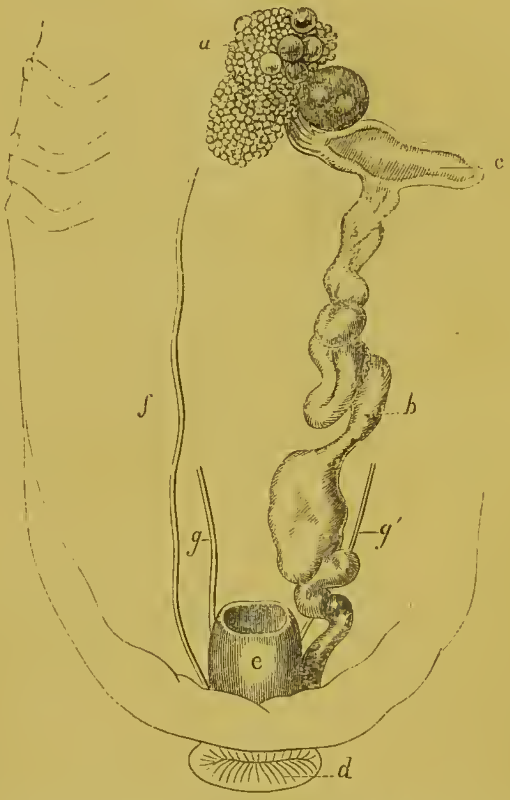
* "History of British Reptiles," pp. 35, 63.

situated close to the upper part of the kidneys; they are composed, as in the Mammalia, of long convoluted tubuli; and they undergo a remarkable development at the epoch of sexual activity, their size being then from twenty to fifty times as great as it is at other periods. The left testis is generally the largest; but we never find it alone developed, and the right testis sometimes equals it in size. The two seminal ducts discharge themselves into the cloaca by two distinct orifices; and a pair of papillary elevations in which these terminate, constitute, in most Birds, the sole rudiment of a penis or intromittent organ. In the Ostrich and some other Birds, however, a distinct penis, furnished with erectile tissue, is present; and the seminal ducts are made to open into a groove upon its upper surface, which, though not completed into a canal, serves by the apposition of its lips to convey the fluid to its extremity, and thus to deposit it within the female passages. When not in a state of erection, the organ is entirely concealed within the cloaca.—The genital apparatus of the female is usually remarkable for its unsymmetrical development; the right ovary and oviduct remaining undeveloped (Fig. 257, *f*), like the left lung of Serpents. Up to a certain period of embryonic life, however, these organs are developed with perfect symmetry on the two sides; and in some of the Raptorial birds, they present an equal development even in adult age. The ovarium, which is attached to the superior or anterior extremity of the right kidney, presents an approach to the structure of this organ in Mammalia; being composed of a 'stroma' or bed of compact fibrous tissue, in the midst of which the ova are evolved; its size is much smaller in proportion to the whole body, except at the period of the development of the ova, than in most of the classes we have yet considered. It is covered by an envelope of its own, and then by the peritoneum; its surface is usually smooth; but, when the ova are being developed, their size causes them to project more or less, so as to form a number of convexities upon it. As the ovisacs enlarge, they gradually project from the ovarium, carrying before them its envelopes; and at last, the ovarium presents almost the appearance of a bunch of grapes (Fig. 257, *a*), the

Fig. 257.



Generative Apparatus of the common *Fowl*;—*a*, single ovary, situated nearly on the median line; *b*, left oviduct; *c*, its funnel-shaped opening; *d*, cloaca; *e*, rectum; *f*, right oviduct atrophied; *g*, *g′*, ureters.

ovisacs hanging from it only by a short peduncle, which contains vessels. Each of these projecting bodies, therefore, contains an ovum, which is enveloped in its ovisac; around this is a thin layer of the stroma; this, again, is enclosed in the proper envelope of the ovarium, consisting of two layers, of which the inner one is vascular; and the peritoneum envelopes the whole. At last the ovum escapes by the rupture of its coverings; and these remain as a sort of cup, which is termed the *calyx*, and which subsequently disappears by absorption.—The oviduct commences by a wide slit (*c*), which receives the ovum at its escape from the ovary; at its lower part it dilates into a thick glandular sac, which secretes the shell; and it terminates in the cloaca (*d*) which is the common outlet of the rectum and of the genito-urinary apparatus.

598. The Ovum, during its passage along the oviduct, receives, as in most of the higher animals, an additional layer of albumen; and this is surrounded by a membrane, which has been commonly regarded as composed simply of the hardened external layer of the albumen, but which has in reality a regular fibrous texture, and is properly homologous with the *chorion* of Mammalia (§ 602). This membrane is composed of two layers, which separate at the obtuse end of the egg, to include a bubble of air; its outer surface is somewhat shaggy, and sends little processes into the shell, which is formed by the calcification of a similar membrane. The outer part of the albumen is extremely watery; but the inner part is viscid, and clings closely to the yolk. The yolk-bag is held in its place within the egg, by two twisted cords, termed *chalazæ*, which appear composed of coagulated albumen; these arise, by a funnel-shaped expansion, from the sides of the yolk-bag opposite the poles of the egg, towards which they pass. In this manner the yolk-bag is prevented from moving towards either end of the egg; but it is permitted to rise towards the side; and, as it is rather lighter than the albumen, it will always approach the shell, whichever side the egg may be resting-on. Further, it is permitted to turn upon its own axis; and hence the *cicatricula* or germ-spot (§ 529), being specifically lighter than the rest, will always be found uppermost. By this very simple contrivance, two necessary conditions are provided-for: the embryo is placed, during its development, in the most advantageous position for receiving the influence of the maternal heat; and it is also brought into the nearest possible relation with the external air, by which the aeration of its fluids is effected. The former condition is indispensable throughout the class, except in a few instances, in which the solar heat is sufficiently intense, or in which artificial heat is designedly substituted (§ 449). The latter, here as elsewhere, is absolutely necessary to the development of the embryo: and the shell, being porous, does not interpose any obstacle to the aeration of the fluids it contains.*—Of the various provisions so remarkable in this class, as in that of Insects, for the protection and maintenance of the

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[*] An attempt was made some time since, to show that no respiratory process takes place in the egg through the medium of the shell-membrane; and that the development of the embryo is carried-on with equal perfection, when the air is completely excluded from the interior. The result, however, was completely fallacious, in consequence of the imperfect nature of the means of exclusion employed; and the very accurate experiments of Schwann leave no doubt, that the access of oxygen is as necessary to the embryo, in all but the very earliest period of development, as it is to the adult. See "Brit. and For. Med. Rev.," Vol. X., p. 229.

young, no detailed account can be here given. In general it is to be remarked, however, that the attention which the young receive after they break the shell, is prolonged in proportion as the plumage, and especially the feathers of flight, are to be of a more perfect character; so that, in this comparatively trifling variation, we have an illustration of the general law,—that the higher the grade of development which the being is ultimately to attain, the more is it assisted in the early stages by its parent,

599. This law is remarkably exemplified in the class *Mammalia*, which unquestionably ranks at the head of the Animal kingdom, in respect to degree of intelligence and general elevation of structure. It is the universal and most prominent characteristic of this class, that the young are retained within the body of the female parent, until they have made considerable progress in their development; that whilst there, they derive their support almost immediately from her blood; and that they are afterwards nourished for some time by a secretion which she affords. In regard to the degree of development attained by the young, however, at the period of their separation from their parent, there is much variation in the different orders; and the lower tribes of the class are so truly intermediate, as to the mode in which this part of the generative function is performed, between the oviparous Birds and Reptiles, and the true viviparous Mammalia, as to be appropriately separated as a distinct sub-class, that of *Ovo-viviparous* or more properly *Implacental* Mammalia. This inferiority of grade manifests itself also in the general development of these animals; especially in their osteology, which presents many oviparous characters, and in the low type of conformation of their brain. At the other extremity in the scale of development, we find Man, in whom the dependence of the offspring on the parent is extended through a much longer period than in any other animal; and this has an obvious relation to the high amount of intelligence which he is destined ultimately to attain.

600. The transition from the Generative apparatus of Birds, in fact, to that of the lowest Mammalia, is by no means abrupt; and the passage from the latter to the highest forms which the class presents, is very gradual.—The 'testes' or spermatic organs of the male usually correspond pretty closely in structure with those of Man; being composed of long tortuous *tubuli seminiferi*, in whose interior the spermatic cells are formed, and the fluid part of the secretion elaborated. They are always developed within the posterior part of the abdominal or in the pelvic cavity, occupying nearly the same situation as the ovaria in the female; and this situation they retain in many of the lower Mammalia, such as the *Cetacea* and *Monotremata*, as also in some Pachydermata and Rodentia. But in most of the other orders, they pass-out into a peculiar prolongation of the abdominal cavity, invested by an extension of its muscles and integuments, which is called the *scrotum;* the cavity of the scrotum frequently communicates freely, however, with that of the abdomen, by an open inguinal canal; and it is only in Man, the Quadrumana, and a comparatively small proportion of the lower orders, that the passage between the two cavities is closed by the contraction of the canal, so as to prevent that descent of the intestines into the scrotum which might take place in the erect posture. The spermatic ducts often communicate

with *vesiculæ seminales*, which appear to serve both as receptacles for the seminal fluid, and as accessory glandular organs; they are, however, frequently wanting. In all instances, the spermatic canals have their final outlet at the extremity of the penis; being carried onwards to it, even where the urinary canal is not continued to that point, which is the case in the *Monotremata.* In this order, the seminal ducts unite with the urethra to form a 'uro-genital canal,' which opens into the cloaca; the penis, however, is perforated by a duct, that subdivides at its bifid extremity, first into two branches, and then into further ramifications which terminate in the papillary elevations of its surface; and it would seem that during coitus, the commencement of the duct of the penis is applied to the orifice of the uro-genital canal, in such a manner that the fluid ejected from this shall be transmitted along the intromittent organ, although the urine discharged from the same orifice at other times passes into the cloaca. Thus, as Prof. Owen remarks, "if the canal of the penis were slit open along its under part, and thus converted into a groove, the male organs of the Ornithorhyncus would be then essentially like those of a Tortoise. The adhesion to the Mammalian type is manifested in a highly interesting manner by the completeness of the urethral canal; whilst the complete separation of the uro-urethral from the semino-urethral passages beautifully illustrates the fact, that the existence of the penis is essentially and subordinately related to the sexual organs, and not to the renal." *—In the *Marsupialia*, the seminal ducts discharge themselves into the urethra, and this is continued onwards to the extremity of the penis; in some members of this order, the penis is bifid, and each half receives a branch of the urethral canal, as in the Monotremata; whilst in others it has a single termination, as in all higher Mammalia.—Various accessory glandular organs are found in the males of most Mammalia, discharging their contents into the urethra, and apparently connected with the generative function; their use, however, is not known.

601. The ovaries of the Mammalian female are always found near the posterior part of the abdomino-pelvic cavity; and they consist of a dense fibrous *stroma*, in the substance of which the ova are developed. These, when mature, are set free by the thinning-away of their envelopes; and are received into the trumpet-shaped dilatations of the oviducts, which canals are known in this class as the 'Fallopian tubes.' The oviducts remain quite distinct from each other in the *Monotremata*, and terminate separately in the uro-genital canal, one on either side of the orifice of the bladder; each of them having first undergone dilatation into a uterine cavity, so that these animals have two completely-distinct uteri. The uro-genital canal opens below into the *cloaca* or common vestibule, its orifice being guarded by a sphincter muscle; and this vestibule also receives the rectum, as in Birds; so that the female generative apparatus of the Monotremata differs but little from that of the highest Ovipara, in which even the uterine dilatation of the oviduct has its representative (Fig. 257). There is not, however, as in Birds, any tendency to the unequal development of the ovaries and their appendages on the two sides.—In the *Marsupialia*, there is a closer approximation of the two lateral sets of organs on the median line; for the oviducts converge

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* "Cyclopædia of Anatomy and Physiology," Vol. III., p. 392.

towards one another, and meet (without coalescing) on the median line; so that their uterine dilatations are in contact with each other, forming a true 'double uterus.' Each uterus, at its lower extremity, opens by an *os tincæ* into a separate vaginal canal; and the two canals diverge again, so as to terminate separately in the uro-genital canal, which receives both their orifices and that of the urinary passage, but terminates externally, without coalescing with the rectum, in a common vestibule. The vaginal canals are frequently furnished, in this order, with peculiar sinuses or dilatations for the reception of the fœtus after it has left the uterus, in which it has undergone a part of its development.—As we ascend the series of 'placental' Mammals, we find the lateral coalescence becoming gradually more and more complete. It shows itself first in the vagina, which is everywhere single, although a trace of separation into two lateral halves is seen in the Mare, Ass, Cow, Pig, and Sloth, in which animals it is traversed, in the virgin state, by a narrow vertical partition. In many of the *Rodentia*, the uterus still remains completely divided into two lateral halves; whilst in others, these coalesce at their lower portion, forming a rudiment of the true 'body' of the humerus in the Human subject. This part increases at the expense of the lateral 'cornua,' in the higher Herbivora and Carnivora; but even in the lower Quadrumana, the uterus is somewhat cleft at its summit, and the 'angles,' into which the oviducts enter, form a considerable part of the whole organ. As we ascend through the Quadrumanous series towards Man, we find the 'body' increasing, and the 'angles' diminishing in proportion; until the original division is completely lost sight of, except in the slight dilatation of the cavity at the points at which the Fallopian tubes enter it. In most Mammalia the female possesses a clitoris, which resembles a rudimentary penis, and which in some instances attains a considerable size.. The urethral canal generally terminates near the base of this organ; but in some of the Marsupialia, this canal seems to be continued as a groove along its under side; and in the Lemming, the Mole, and some of the lower Quadrumana, it is completed into a tube, which passes along the whole length of the clitoris, just as the urethra of the male traverses the penis.—The *Marsupialia* are remarkable for the peculiar addition to their generative apparatus, which consists of a sac or pouch upon the front of the pelvis, formed by a pair of folds of the integument, and covering-in the mammary glands and nipples; and the function of this 'marsupium' is obviously to afford protection to the young animal, in that state of extreme immaturity which characterizes it at the date of its emersion from the uterus and for some time afterwards; during which period it is clinging to the nipple, at first apparently almost unpossessed either of sensibility or of power of movement, but gradually acquiring the ability to sustain an independent existence.

602. The Ovum itself corresponds, in all essential characters, with that of Oviparous animals;—chiefly differing in its minute size, in proportion to that of the ovisac (§ 526). Its external envelope is thicker than the ordinary yolk-bag of oviparous animals; and has received the name of *Zona pellucida*, from its appearing under the microscope (when the ovum is flattened by compression) as a broad transparent ring *

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* This *Zona pellucida* has been described by some writers under the name of *chorion*; the true chorion, however, is afterwards formed around it.

(Fig. 221, *m v*). In the immature ovisac, the space between its inner layer and the ovum is for the most part filled-up with cells; these, however, gradually dissolve-away, especially on the side nearest the surface of the ovary, whilst an albuminous fluid is effused from the deeper part of the ovisac, which pushes before it the residual layer that immediately surrounds the ovum, forming the *discus proligerus,* and thus carries it against the opposite wall. At this period, the vascular tunic enveloping the ovisac, which is derived (as in Birds) from the parenchyma of the ovary, is acquiring great thickness and consistency; and the two membranes together form the structure known as the *Graafian Follicle,* which was formerly regarded as peculiar to the Mammalia, but which is really analogous to the inner part of the *calyx* of Birds and other Ovipara.* When the ovum has attained its full development, it is carried to the side of the Graafian follicle nearest the surface of the ovary, by the effusion of fluid on the side more deeply imbedded; and there it remains, until the rupture of the envelope allows of its exit from the cavity. This rupture is preceded by a gradual thinning of these membranes at that point; but on the opposite side, the outer or vascular tunic becomes much thickened; and a fleshy substance of a reddish-yellow colour (entirely composed of cells) sprouts from the interior of the ovisac, which it gradually fills after the discharge of the ovum, forming the *corpus luteum.*—When set-free from the ovarium, the ovum is received into the Fallopian tube; and its fertilization appears to take place almost immediately on its entrance into that canal, if it have not been previously accomplished. During its passage towards the uterus, it acquires an additional envelope, the true *Chorion,* which has subsequently to perform very important functions in the nutrition of the embryo. This is at first seen as a layer of cells in contact with the outer surface of the Zona pellucida; it usually, however, imbibes fluid, which separates it from the Zona pellucida; and a change takes place in its own structure, by the alteration in the form of its cells, which extend themselves and interlace in various directions, so as to give the fabric a fibrous texture, and to produce asperities on its outer surface. In its situation and mode of production, the chorion is evidently homologous with the *membrana testæ* of Birds; and the fluid which it absorbs is comparable to the albumen of the egg of the latter. The connection between the two is clearly established by the ovum of the *Monotremata,* in which there is a distinct albumen around the yolk-bag, contained in a membrane, which, —as these ova are not to be incubated, but are destined to receive their early development within the uterus,—must subsequently become the chorion. In all Mammiferous animals, the oviduct, instead of immediately conveying the ovum out of the body, deposits it in the uterine receptacle provided for its further development; within which it forms a new connection with the parent, and is supplied with nutriment from the fluids of the latter, until it has arrived at a state of completeness usually corresponding with that which the Chick presents, when it emerges from its shelly covering.

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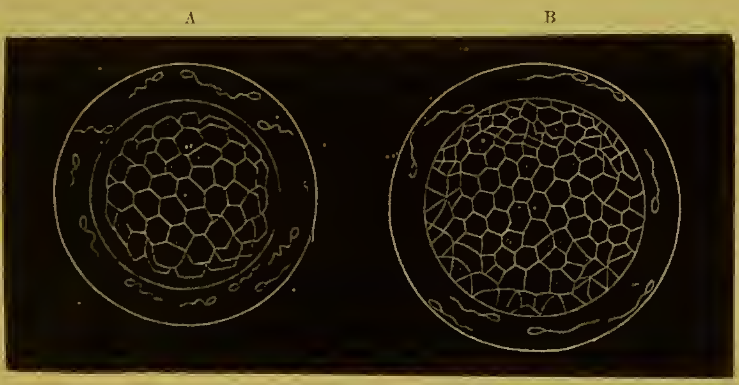
* It is maintained by Reinhardt ("Kölliker and Siebold's Zeitschrift," Band III.), that the whole Graafian vesicle of the Mammal, with its contents, is the real homologue of the Yolk-bag of the Bird; the 'food-yolk' of the latter being represented by the cellular mass which surrounds the Zona pellucida of the former, and which is afterwards developed into the 'corpus luteum.'

603. It now remains for us to consider the peculiarities which distinguish the development of the embryo of the *Vertebrata,* from the process already described in the other Sub-Kingdoms. These peculiarities chiefly consist in this;—that the permanent structure is usually developed from a very limited portion only of the 'mulberry-mass' (§ 529); whilst the remainder of this, with that extension which it forms over the large mass of 'food-yolk' that forms the bulk of the vitelline body in Birds and Fishes, and probably in the higher Reptiles, has but a very subordinate and temporary office,—being destined (like the cotyledonous expansion of the higher Plants) solely for the imbibition and assimilation of nutriment, during the early period of evolution. In the ova of Batrachia and Mammalia, there is no 'food-yolk' in addition to the 'germ-yolk;' and as the entire vitellus consists of the latter, the whole of it is involved in the process of segmentation. This arrangement, which is common to them with Invertebrata generally (save the highest of the Articulated and Molluscous series), appears to be related to the fact, that in neither of these two cases is the development of the embryo carried-on far at the expense of the vitellus; for that of the Frog proceeds no further within the ovum, than to the production of a fish-like larva; and the continued development of the Mammal is very early provided-for by a different arrangement.—The evolution of the fractions of the vitellus (Fig. 258, A) into true cells, by the formation of a cell-wall around them (§ 529), takes place soonest, as well as most completely, at its peripheral portion; and its cells arrange themselves, in the act of formation, into a kind of membrane lining the yolk-bag, at the same time assuming a pentagonal or hexagonal shape from mutual pressure, so as to resemble pavement-epithelium (B). Of the globular masses of the interior, those nearest the surface seem to be developed into true cells, and to increase the thickness of the membrane already formed by the more superficial layer; but the spherules of the interior appear for the most part to liquefy again; so that the embryonic mass is now in the condition of a cellular stratum, known as the 'germinal membrane,' inclosing a liquid yolk,—a condition which is closely paralleled by the embryo of Zoophytes,

FIG. 258.

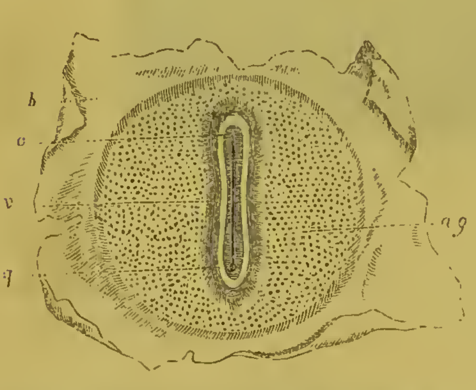


Later stage in the segmentation of the yolk of the *Mammalium Ovum;* at A is shown the "mulberry mass" formed by the minute subdivision of the vitelline spheres; at B, a further increase has brought its surface into contact with the vitelline membrane, against which the spherules are flattened.

previously to the formation of the oral aperture.—In the ova of Fishes and Birds, however, and probably in those of true Reptiles, there is a large food-yolk, in which the segmentation does not take place; and the mode in which this becomes enclosed by the 'germinal membrane,' is by the extension of the peripheral portion of the *cicatricula*, which seems to be formed by the segmentation of the 'germ-yolk.'—The 'germinal membrane' is sometimes termed the *blastoderma;* and the new envelope which is formed by it, between the vitellus and its original sac, has been termed by Bischoff the *blastodermic vesicle.* This vesicle, very soon after its formation, presents at one point an opaque, roundish spot, which is produced by an accumulation of cells and nuclei of less transparency than elsewhere; within this, which is termed the *area germinativa*, all the structures of the permanent organism originate. The germinal membrane increases in extent and thickness, by the formation of new cells (whose mode of production has not been clearly made-out); and it subdivides into two layers, which, although both at first composed of cells, soon present distinctive characters, and are concerned in very different ulterior operations. The outer one of these is commonly known as the *serous* layer; but being the one in whose substance the foundation is laid for the vertebral column and the nervous system, it is sometimes called the *animal* layer. The inner one is usually known as the *mucous* layer; and being the one chiefly concerned in the formation of the nutritive apparatus, it is sometimes called the *vegetative* layer. This division is at first most evident in the neighbourhood of the area germinativa; but it soon extends from this point, and implicates nearly the whole of the germinal membrane.

604. The 'area germinativa' (Fig. 259, *a g*), at its first appearance, has a rounded form; but it soon loses this, first becoming oval, and then pear-shaped. While this change is taking-place in it, there gradually appears in its centre a clear space, termed the *area pellucida;* and this is bounded externally by a more opaque circle (whose opacity is due to the greater accumulation of cells and nuclei in that part, than in the area pellucida), which subsequently becomes the *area vasculosa.* In the formation of these two spaces, both the serous and mucous layers of the germinal membrane seem to take their share; but the foundation of the embryonic structure, known as the *primitive trace*, is laid in the serous lamina only. This consists in a shallow groove, lying between two oval masses (*v*), known as the *laminæ dorsales.* The form of these changes with that of the area pellucida; at first they are oval, then pyriform, and at last become of a guitar-shape. At the same time, they rise more and more from the surface of the area pellucida, so as to form two ridges of higher elevation, with a deeper groove between them; and the summits

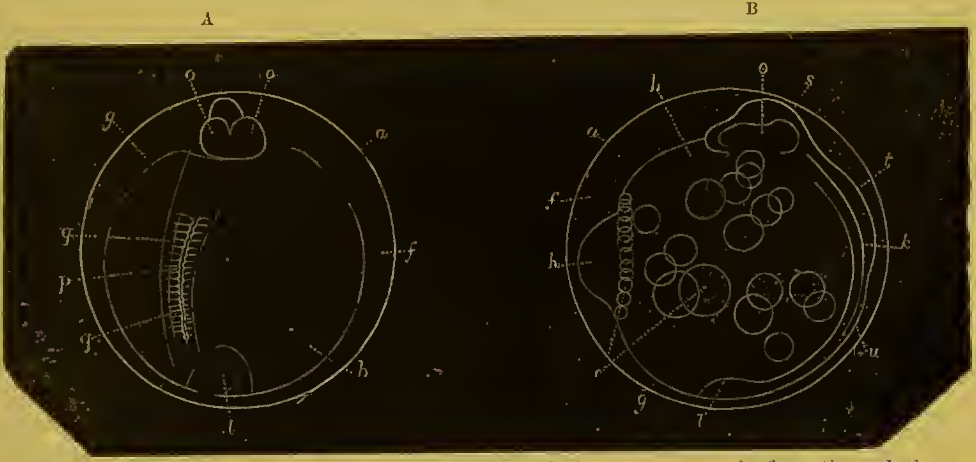
Fig. 259.



The germ and surrounding parts, from a more advanced *Uterine Ovum;*—*b*, blastoderma, or germinal membrane; *a g*, area germinativa; *c*, cephalic extremity of the germ; *v*, first indications of vertebræ; *q*, caudal extremity.

of these ridges tend to approach each other, and gradually unite, so as to convert the groove into a tube. At the same time, the anterior portion of the groove dilates into three recesses or vesicles, which indicate the position of the three principal divisions of the Encephalon, afterwards to be developed as the *prosencephalon*, the *mesencephalon*, and the *epencephalon* (Fig. 262, B, *x*, *y*, *z*). The most internal parts of these 'laminæ,' bounding the bottom and sides of the groove, appear to furnish the rudiments of the nervous centres which this cranio-vertebral canal is to contain; whilst the outer parts are developed into the rudiments of the vertebral column and cranium. Even before the 'laminæ dorsales' have closed over the primitive groove, a few square-shaped, at first indistinct, plates, which are the rudiments of vertebræ (Fig. 260, A, *q*, *q*), begin to appear at about the middle of each. The position of the bodies of the vertebræ is indicated at this period, by a distinct cylindrical rod of nucleated cells, termed the *chorda dorsalis;* and this retains its embryonic type in the Myxinoid Fishes. While this is going-on, an accumulation of cells takes place between the two laminæ of the germinal membrane at the 'area pellucida;' and these cells speedily form themselves into a distinct layer, the *vascular* lamina, in which the first blood-vessels of the embryo are developed, as will be presently described (§ 605). From the dorsal lamina on either side, a prolongation passes outwards and then downwards, forming what is known as the *ventral lamina;* in this are developed the ribs and the transverse processes of the vertebræ; and the two have the same tendency to meet on the median line, and thus to close-in the abdominal cavity, which the dorsal laminæ have to inclose the spinal cord. At the same time, the layers of the 'germinal membrane,' which lie beyond the extremities of the embryo, are folded-in, so as to make a depression on the yolk; and their folded margins gradually approach one another under the abdomen. The first rudiment of the intestinal canal presents itself as a channel along the under surface of the embryonic mass, formed by the rising-up of the inner layer of the germinal membrane into a ridge on either side. The two ridges gradually

FIG. 260.



Ovum of *Coregonus palæa*, eleven days after fecundation; A, as seen in front through the transparent ovum; B, as seen sideways;—*a*, shell-membrane; *b*, yolk; *e e*, oil-globules; *f*, albumen; *g g*, vitelline membrane; *h*, yolk-vesicle; *k*, trunk of the embryo; *l*, tail; *o o*, optic lobes; *p*, chorda dorsalis; *q q*, vertebral divisions; *u*, curve of the trunk.

arch-over and meet, so as to form a tube, which is thus (so to speak) pinched-off from the general vitelline sac; but it remains in connection with this by means of an unclosed portion, which constitutes the 'vitelline duct.' In oviparous animals generally, the yolk-bag, as it is emptied of its contents, is gradually drawn into the abdominal cavity; but in Mammalia, and also in the higher Cartilaginous Fishes, it is cut-off from the intestine by the obliteration of the vitelline duct, and by the complete closure of the abdominal parietes around the peduncle. The minute yolk-bag of Mammalia is known under the name of the 'umbilical vesicle.'

605. Whilst these new structures are being produced, a very remarkable change is taking place in that part of the serous lamina which surrounds the 'area pellucida.' This rises-up on either side in two folds; and these gradually approach one another, at last meeting in the space between the general envelope and the embryo, and thus forming an additional investment to the latter. As each fold contains two layers of membrane, a double envelope is thus formed; of this, the outer lamina adheres to the general envelope; whilst the inner remains as a distinct sac, to which the name of *Amnion* is given. (See Figs. 261 and 264.) This takes place during the third day in the Chick; and at about the same period, a very important provision for the future support of the embryo begins to be made, by the development of blood-vessels and the formation of blood. Hitherto the embryonic structure has been nourished by direct absorption of the alimentary materials supplied to it by the yolk; in the same manner as the simplest Cellular Plant is developed at the expense of the carbonic acid, moisture, &c., which it obtains for itself from the surrounding elements. But its increasing size, and the necessity for a more free communication between its parts than any structure consisting of cells alone can permit, call for the development of vessels, through which the nutritious fluid may be conveyed. These vessels are first seen in that part of the Vascular lamina of the germinal membrane, which immediately surrounds the embryo; and they form a network, bounded by a circular channel, which is known under the name of the *Vascular Area* (§ 254, Fig. 133). This gradually extends itself, until the vessels spread over the whole of the membrane containing the yolk. The first blood-discs appear to be formed from the nuclei of the cells, whose cavities have become continuous with each other to form the vessels; and from these, the subsequent blood-discs of the first series are probably generated. This net-work of blood-vessels serves the purpose of absorbing the nutritious matter of the yolk, and of conveying it towards the embryonic structures, which are now in process of rapid development. The first movement of the fluid is *towards* the embryo; and this can be witnessed before any distinct heart is evolved. The same process of absorption from the yolk, and of conversion into blood, probably con-

FIG. 261.

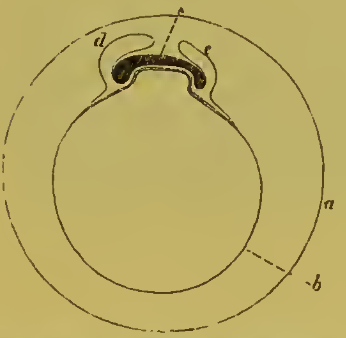


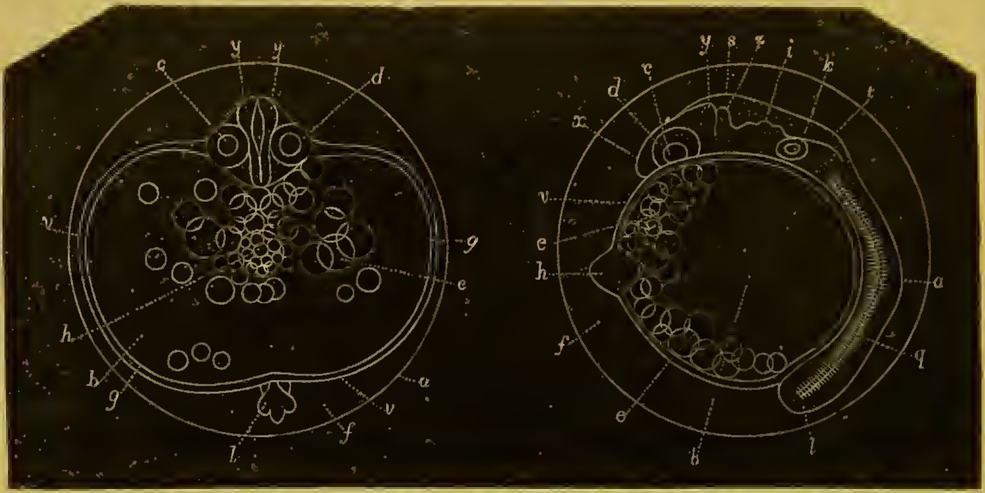
Diagram of Ovum at the commencement of the formation of the Amnion;—*a*, chorion; *b*, yolk-sac; *c*, embryo; *d*, and *e*, folds of the serous layer rising up to form the amnion.

tinues as long as there is any alimentary material left in the sac. The mode in which the Heart is formed, and the subsequent phases of its development, as well as of that of the principal Blood-vessels, have been already described (§§ 255-260); it is only necessary here to add, that the mass of cells in which it originates, may be considered as a thickened portion of the vascular layer. The trunks which connect the circulating system of the embryo with that of the 'vascular area,' are called *Omphalo-Mesenteric*, *Meseraic*, or *Vitelline* vessels. It was formerly believed, that the nutrient matter of the yolk passes directly through the vitelline duct, into the (future) digestive cavity of the embryo, and is from it absorbed into its structure; but there can now be little doubt, that the vitelline vessels are the real agents of its absorption, and that they convey it to the tissues in process of formation. They do, in fact, correspond to the Mesenteric veins of Invertebrated animals, which are the sole agents in the absorption of nutriment from their digestive cavity (§ 189); and the blastodermic vesicle may be regarded as the temporary stomach of the embryo,—remaining as the permanent stomach in the Radiated tribes. Previously to the ninth day of incubation (in the Fowl's egg), a series of folds are formed by the lining membrane of the vesicle, which project into its cavity; these become gradually deeper and more crowded, as the bag diminishes in size by the absorption of its contents. The vitelline vessels that ramify upon the vesicle, send into these folds (or valvulæ conniventes) a series of inosculating loops, which immensely increase the extent of this absorbing apparatus. But these minute vessels are not in immediate contact with the yolk; for there intervenes between them a layer of nucleated cells, which is easily washed away. It was from the colour of these, communicated to the vessels beneath, that Haller termed the latter *vasa lutea;* when the cellular layer is removed, the vessels present their usual aspect. There seems good reason to believe, that these cells are the real agents in the process of absorbing and assimilating the nutritive matter of the yolk; and that they deliver this up to the vessels, by themselves undergoing rupture or dissolution, being replaced by newly-formed layers.

606. The development of the embryo of *Fishes* takes place without any further change of plan; the nutrient material supplied by the yolk being gradually taken into the circulation, through the medium of the germinal membrane, and being applied to the nutrition of the various tissues and organs which successively make their appearance. Up to the time of the emersion of the fœtal fish from the egg, the aeration of the blood is provided-for in no other way, than by its distribution upon the surface of the yolk-bag; and even after it has come forth, whilst the yolk-bag is still far from being emptied, and hangs-down from its abdomen, and the gills have not yet come into play, the dispersion of the blood over the vascular area still serves to aerate it, as well as to enable it to absorb the nutritive contents yet remaining to be appropriated. In most of the Osseous Fishes, the blood-vessels which ramify upon the yolk-bag may be regarded as part of the portal system; for they branch-off from the intestinal veins, and return into the vena cava. As the yolk diminishes in size, and the permanent respiration is established, the blood is transmitted more directly through the liver to the heart, by the enlargement of vessels that were at first capillary, into regular trunks. In the higher Carti-

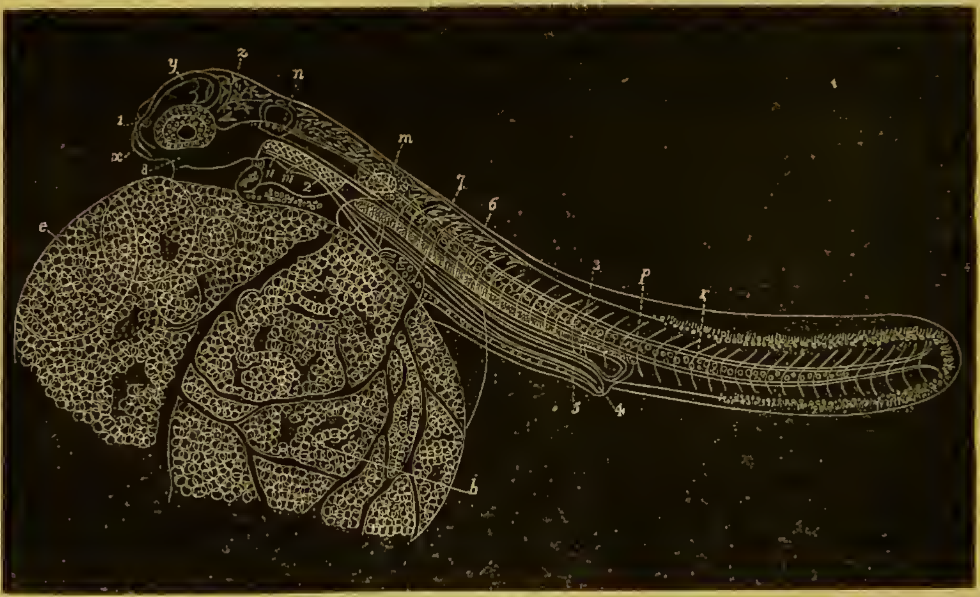
laginous fishes, however, the blood sent to the respiratory surface is derived from an arterial trunk, as in all the higher Vertebrata.—The general course of the development of the principal organs in Fish, may be understood from the accompanying figures; the history of the evolution of

Fig. 262.



Ovum of *Coregonus palæa*, sixteen days after impregnation;—A, seen in front;—B, seen sideways;—*a*, shell-membrane; *b*, yolk; *c*, crystalline lens; *d*, choroidal system; *e e*, oil-globules; *f*, albumen; *g*, vitelline membrane; *h*, yolk-vesicle; *i*, keel of the enecphalon; *k*, ear; *l*, tail; *q*, vertebral divisions; *s*, cephalic bend; *t*, nuchal bend; *v*, epidermoidal stratum; *x*, prosencephalon; *y*, mesencephalon; *z*, epencephalon.

Fig. 263.



Embryo of *Coregonus palæa*, thirty-three days after fecundation;—*b*, yolk; *e*, oil-globules; *m*, pectoral fin; *n*, ear; *p*, chorda dorsalis; *r*, sheath of the dorsal chord; *x*, prosencephalon; *y*, mesencephalon; *z*, epencephalon; 1, pineal gland; 2, buccal intestine; 3, ureter; 4, anus; 5, ventral intestine; 6, kidneys; 7, liver; 8, mouth; II and III, second and third branchial fissures.

each principal organ has been already given under its own head; with the exception of that of the Nervous system, which will be found in its proper place (§§ 663, 667).

607. In all the higher Vertebrata, we find that at an early period of embryonic development, provision is made for a more effectual performance of the Respiratory function. This consists in the development of a peculiar membrane, the *Allantois;* which sprouts-forth from the caudal extremity of the embryo, at first as a little mass of cells, whose interior is soon observed to be hollow; and which continues to enlarge, until it surrounds the entire embryo (Figs. 264--267). In *Reptiles* and *Birds*, it extends itself around the yolk-sac, intervening between it and the membrane of the shell; and the porosity of the latter allows the air to have free access to the blood, which is copiously distributed upon it. It is a remarkable circumstance, that this membrane should not merely serve as a respiratory organ, but that it should also stand to the Corpora Wolffiana, or temporary kidneys, in the light of a receptacle for their secretion, or urinary bladder. The greater portion of this allantois is afterwards cast-off by the contraction of its pedicle; but a part of its root is usually retained, to be converted into the permanent urinary bladder.—In *Mammalia*, however, the chief office of the allantois is to convey the vessels of the embryo to the internal surface of the Chorion (Fig. 266); the tufts of which are rendered vascular by the penetration of these vessels into them (Fig. 267); and in this mode the embryo is nourished for a time, the absorbent tufts drawing their supplies by endosmose from the very vascular lining of the uterus.

Fig. 264.*

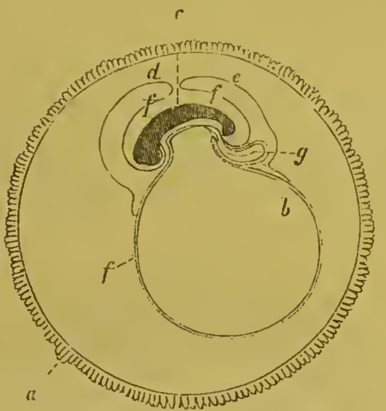
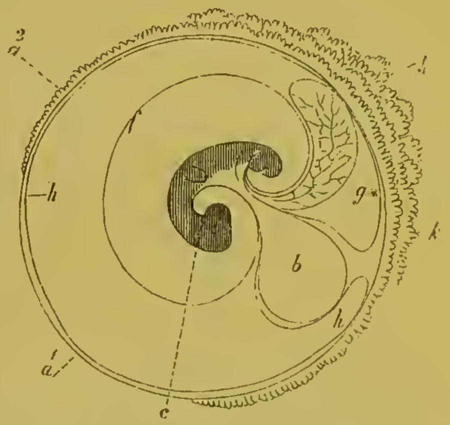


Fig. 265.†



* Diagram of *Human Ovum*, with the Amnion in process of formation:—*a*, the chorion; *b*, the yolk-bag, surrounded by the serous and vascular laminæ; *c*, the embryo; *d*, *e*, and *f*, external and internal folds of the serous layer, forming the amnion; *g*, incipient allantois.

† Diagram representing a *Human Ovum* in second month:—*a* 1, smooth portion of chorion; *a* 2, villous portion of chorion; *k*, *k*, elongated villi, beginning to collect into Placenta; *b*, yolk-sac or umbilical vesicle; *c*, embryo; *f*, amnion (inner layer); *g*, allantois; *h*, outer layer of amnion, coalescing with chorion.

608. Whilst the foregoing changes have been taking place in the ovum, the mucous membrane lining the Uterus has undergone an important change; for it has become extremely thick and vascular, and its follicles are greatly enlarged, and appear to secrete a nutritive material from the blood. When the tufts of the chorion come into apposition with it, they insinuate themselves into these glandular follicles; and absorb the material which has been elaborated by them for the support of the embryo. Each villus of the chorion contains a capillary loop; this is enclosed in a

layer of cells, and this again in a lamina of basement-membrane; the whole constituting the *fœtal* tuft. On the other hand, this tuft is in apposition with a layer of cells covering the orifices of the uterine glandulæ, and these lie upon the basement-membrane of its mucous lining; forming the *maternal* portion of the apparatus. Such is the highest form which it assumes in the *Implacental* Mammalia (§ 68); the ovum being ejected from the uterus, before any further changes have taken place. In the higher orders, however, we find such a concentration of this arrangement in one or more spots, as is adapted to bring the fœtal and the maternal blood-vessels into closer approximation. This is accomplished, in the Ruminants, by an enlargement and multiplication of the vascular tufts at several points of the surface of the chorion, so as to form what are termed the *fœtal cotyledons;* and these come into relation with a corresponding series of *maternal cotyledons*, formed by the enlargement and multiplication of the blood-vessels of the lining membrane of the uterus. No inosculation takes place between these two sets of vessels; but the loopings of each are received into the interspaces between those of the other; and each tuft is covered with its own layer of basement-membrane and of cells. In Man, however, and in the Quadrumana, Carnivora, and other orders, a still more concentrated arrangement is found. The vascular tufts are enormously developed from one portion only of the chorion; and they dip-down, as it were, into a cavity, whose inner wall is formed by an extension of the lining membrane of the large veins or sinuses of the uterus. The former, which are the ultimate ramifications of the umbilical arteries,

Fig. 266.*

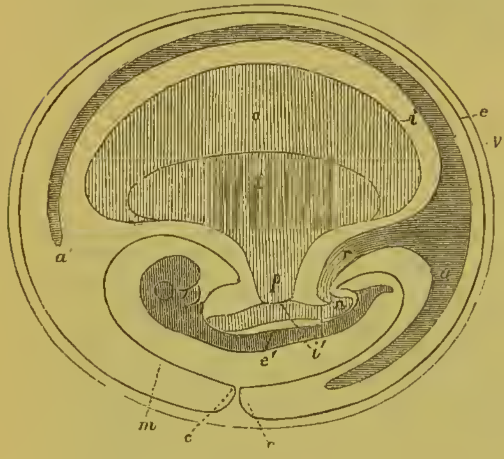
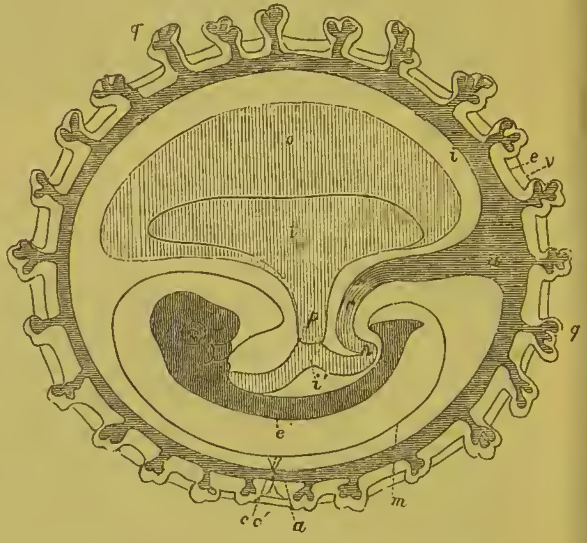


Fig. 267.†

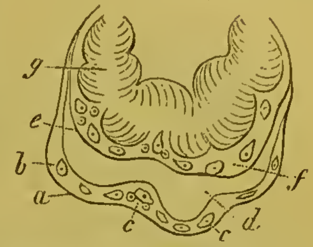


* Diagram of *Human Ovum* in a more advanced stage;—*a a'*, the Allantois developing itself around the embryo; *c c'*, the cephalic and caudal prolongations of the amniotic sac, nearly united; *e*, serous layer of the germinal membrane; *e'*, vertebral structure of the fœtus; *i*, mucous layer of the germinal membrane, partly converted into the rudimentary intestine *i'*, and partly forming the umbilical vesicle *o*; *m*, portion of the serous layer of the germinal membrane reflected to form the amnion; *n*, rudimentary portion of the intestine, representing the rectum; *p*, pedicle of the umbilical vesicle; *r*, pedicle of the allantois; *t*, limit of the area vasculosa; *v*, vitelline membrane.

† Diagram of *Human Ovum* still more advanced, the two prolongations of the Allantois having now met and united at *a*, and the amniotic sac being now complete; the external layer of the germinal membrane, *e*, is now disappearing; vascular villosities, *q q*, are being developed from the allantois; and the intestine *i'* is forming its first loop.—The other references as in the preceding figure.

constitute the *fœtal* portion of the *Placenta* (as this compound organ is termed); whilst the latter, which constitutes its *maternal* portion, is irregularly subdivided by partitions, formed by reflexions of its wall over the fœtal tufts; and each of these reflexions carries with it an extension of the cellular layer that covers the mucous surface, so that the extremity of every loop of fœtal vessels forming a placental villus is invested first by a fœtal, and then by a maternal, layer of cells, a space being usually observed to intervene between them (Fig. 268). The blood is conveyed into the placental cavity by the 'curling arteries' of the uterus; and after it has been brought into relation with that of the fœtus, it is returned to the uterus by large apertures communicating with its sinuses. Thus the placental tufts, in which the fœtal blood is circulating, are bathed (as it were) in the maternal blood, just as the branchiæ of aquatic animals are bathed in the medium they inhabit; and an interchange can freely take place by endosmose between the two fluids, although no more direct communication exists between the two systems of vessels. This interchange is subservient to two most important purposes. The fœtal tufts draw from the maternal blood the materials which are required for the nutrition of the embryo, these materials having been first elaborated by the two sets of intervening cells; and in this character, the fœtal tufts resemble the villi of the intestinal surface, which dip-down into the fluids of the alimentary canal, and absorb the nutritive materials which they furnish. But the placenta serves also as the instrument for the depuration of the blood of the fœtus, especially by the respiratory process; for the aerated blood of the mother will necessarily impart oxygen to that of the fœtus, and will carry-off its carbonic acid; so that in this respect the fœtal tufts may be likened functionally, as well as structurally, to the gills of aquatic Animals. But it is probable that during the early stages of embryonic life, before the proper depurating organs of the fœtus have come into full activity, other excretory matter may be got-rid-of through the same channel; and there even seems a strong probability, that the fœtal blood may so react upon the maternal, as to communicate to it some of the properties which it has derived from its male parent. Such, at least, seems the most feasible explanation of the fact, which has now been observed to take place in a great number of instances, that if a mare, cow, bitch, or other mammiferous female (not even excepting the human species), be impregnated in the first instance by a male possessing some marked peculiarity, and on subsequent occasions by a different male, the offspring of the second parentage will bear in greater or less degree the characters of the first; these peculiarities becoming less and less obvious on each successive occasion.*

Fig. 268.



Extremity of a *Placental Villus*:—*a*, external membrane of the villus, continuous with the lining membrane of the vascular system of the mother; *b*, external cells of the villus, belonging to the placental decidua; *c*, *c*, germinal centres of the external cells; *d*, the space between the maternal and fœtal portions of the villus; *e*, the internal membrane of the villus, continuous with the external membrane of the chorion; *f*, the internal cells of the villus, belonging to the chorion; *g*, the loop of umbilical vessels.

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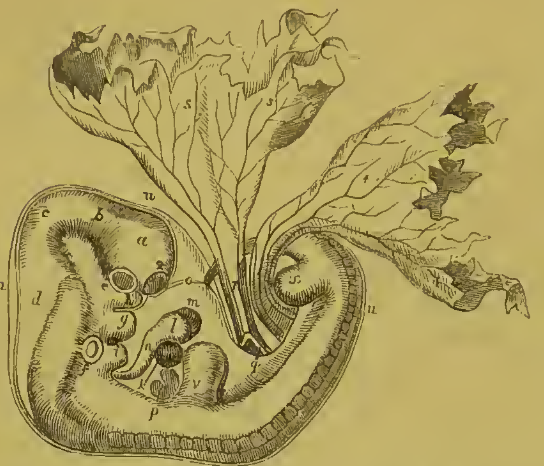
* See the very ingenious papers on this subject by Dr. Harvey, in the "Edinb. Monthly Journal" for 1849 and 1851; and his pamphlet "On a remarkable effect of Cross-breeding," Edinburgh, 1851.

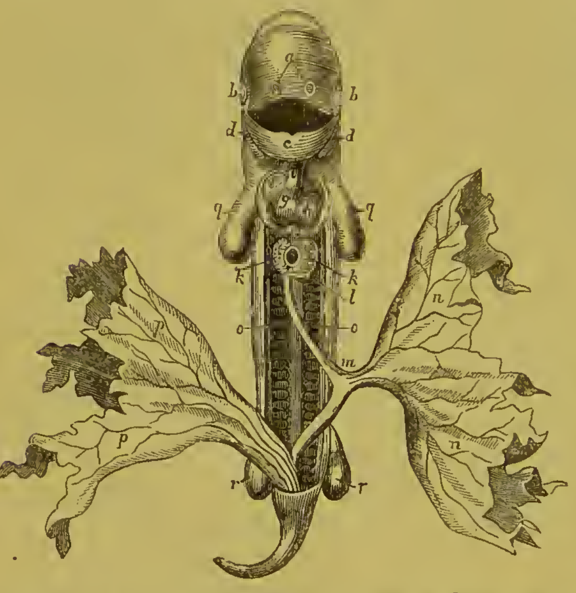
609. Notwithstanding the peculiarity of the provision which is made in Mammalia for the nutrition of the embryo, the earlier part of its course of development presents little to distinguish it from that of the inferior classes. It may, in fact, be said, that all the most important parts of the apparatus of Organic life, and even the fundamental portions of that of Animal life, are developed upon the same general plan in all Vertebrata; and that the special peculiarities of each class only gradually evolve themselves. The conditions under which the alimentary canal (§§ 162, 604), the heart and blood-vessels (§§ 254—260), the liver (§ 412), the corpora wolffiana (§ 422), the vertebral column (§ 604), the nervous centres (§ 663), and the ear and eye (§§ 716, 724), first present themselves, exhibit no essential differences in the Fish, Reptile, Bird, or Mammal; and the first considerable divergence from the common type is shown in that alteration in the structure of the Heart, and in the arrangement of the great vessels, which distinguishes the air-breathing Vertebrate from the Fish; whilst in the latter, the original conformation is retained, and is made subservient to the distribution of the blood in the arterial filaments. So again, at a later period, the Corpora Wolffiana give place in the air-breathing Vertebrate to the permanent Kidneys, but remain persistent in the Fish. In like manner, the course of development of the vertebral elements very early shows those peculiarities, which are charac-

FIG. 269.



Embryo of *Dog*, twenty-five days after the last copulation, enlarged three times;—*a*, prosencephalon; *b*, deutencephalon; *c*, mesencephalon; *d*, epencephalon; *e*, eye; *f*, auditory vesicle; *g*, *h*, *i*, visceral arches; *k*, right auricle; *l*, right ventricle; *m*, left ventricle; *n*, bulbus aorticus; *o*, pericardium; *p*, liver; *q*, loop of intestine, communicating through *r*, the ductus omphalo-mesentericus, with *s*, *s*, the umbilical vesicle; *t*, allantois; *u*, amnion; *v*, anterior extremity; *x*, posterior extremity; *z*, nose.

FIG. 270.



The same Embryo, straightened, and seen in front;—*a*, *a*, nostrils; *b*, *b*, eyes; *c*, *c*, first visceral arch, forming the lower jaw; *d*, *d*, second visceral arches; *e*, right auricle; *f*, left auricle; *g*, right ventricle; *h*, left ventricle; *i*, aortic bulb; *k*, *k*, liver, between the two lobes of which is seen the divided orifice of the omphalo-mesenteric vein; *l*, stomach; *m*, intestine, communicating with the umbilical vesicle *n*, *n*; *o*, *o*, corpora Wolffiana; *p*, allantois; *q*, *q*, anterior extremities; *r*, *r*, posterior extremities.

teristic of the type of the Fish; whilst it is not until a subsequent period, that in these or any other parts (save in the provisions already described for the nutrition of the fœtus and the aeration of its blood) is there anything that can be accounted distinctive of either of the higher classes of Vertebrata.—The accompanying figures exhibit an early phase of the evolution of the Mammalian embryo, in which most of the organs are in a very rudimentary condition. It is in a state not much further advanced than this, that the embryo of *Monotremata* and *Marsupialia* is expelled from the uterus; in the higher orders, however, it is retained in that cavity, and continues to derive its support through the placenta, until nearly all the principal organs in the body, save the generative, are prepared for the active performance of their respective functions. Still there are considerable differences in the degree of independence manifested by the young Mammalia of different orders at the epoch of their birth; those of most *Carnivora* and *Rodentia*, for example, coming into the world in a feeble condition, their eyelids being adherent, their movements feeble, and their calorifying power low; whilst those of *Ruminants* possess the use of the visual sense from the first, speedily acquire considerable locomotive power, and can maintain their own heat.

610. Although nothing is certainly known in regard to the causes which influence the Sex of the offspring, some facts which have been observed on this curious subject are worthy of being here adverted-to, with the purpose of stimulating further enquiry. It is stated by Mr. Knight, that several kinds of monœcious Plants can be made to produce solely-male or solely-female flowers, by regulating the quantity of light and heat under which they are grown. If the heat be excessive, compared with the quantity of light which the plant receives, male flowers only appear;—but if light be in excess, female flowers alone will be produced. In this case, it seems likely that both sets of sexual organs exist in a rudimentary state; and that the one or the other kind is developed according to external circumstances. To the same industrious experimenter we owe some interesting facts in regard to Animals, to which this explanation is not applicable. He remarks that, in flocks or herds of domesticated quadrupeds, it is no uncommon thing to meet with *females*, whose offspring is almost invariably of the same sex, although it may have resulted from intercourse with several different males; whilst, on the other hand, he has never met with *males* that exhibited any such uniformity in the sex of their offspring with different females. Hence he concludes that the female parent exercises the chief influence in determining the sex. An experiment upon the fecundation of Birds, which he states to have been frequently repeated, gave the following curious result. When the female was kept without intercourse with the male, up to nearly the time of laying, so that the eggs had advanced very far in their development at the time of fertilization, the proportion of males among the offspring was very large,—commonly about six out of seven.* Some observations which have been made on the Human species tend to show, that there is a probability of a majority in the number of one sex over the other, according to the relative ages of the parents;—the male children predominating in those families in which the father's age is considerably above the mother's, and *vice versâ*.†

* "Selections from Mr. Knight's Physiological Papers," pp. 347, 357.
† Quetelet "Sur L'Homme," Tom. I., pp. 52, 53.

611. In no tribe of animals save Mammalia, do we find that the young are nourished exclusively, for some time after their birth, by a fluid secreted from the blood of the maternal parent; the nearest approach to this is presented by the *Pigeon*, whose 'crop' during the breeding season secretes a milky fluid, which is mingled with the macerating grains, and is returned with them to the mouth, to be imparted to the young. The Mammary Glands present, in the different orders, a considerable variety, both in situation and in grade of development. In the greater part of the class, they are found in close connection with the generative apparatus, their orifices in the Cetacea being very near the outlets of the rectum and vagina, whilst in many other groups (as the Ruminants) they are only a little removed from these; but as we ascend towards Man, we find them occupying a more and more advanced position on the trunk, until they are limited, as in him, to the pectoral region. In complexity of structure, also, the advance is alike gradual: for the Mammary glands of the *Ornithorhyncus* are of the most simple conformation, consisting of a mere cluster of isolated follicles without any nipple (Fig. 171); those of the *Cetacea* are but little above them in structure, and the nipples are buried in a cleft of the integument; whilst in the higher Mammalia, these glands are formed upon a very elaborate type, and the nipples are prominently developed, so as to be received into the mouth of the offspring, which draws-forth the secretion by suction. The most remarkable development of the nipple, however, is found in the *Marsupialia*, in which it serves for the attachment of the 'marsupial fœtus,' and for the conveyance into its œsophagus of the secreted fluid, which is here expelled from the mammary gland by the action of a compressor muscle. A similar expulsor action seems to be exercised by the abdominal muscles of the *Ornithorhyncus;* for although (as Prof. Owen has shown) the young possesses flexible lips instead of the horny bill of the adult, with a tongue adapted for suction, these can scarcely act effectually without a nipple, and the nutriment is probably imparted and received by both actions conjointly.

612. The *Milk* of most Mammalia consists of Water, holding in solution a peculiar albuminous substance termed Caseine, and various Saline ingredients, together with (in most instances) a certain form of Sugar; and having Oleaginous globules suspended in it. The most important difference between Caseine and Albumen consists in the fact, that the former *is not* coagulated by heat, which precipitates the latter; and that it *is* coagulated by acetic acid, which has no effect upon the latter. Caseine is very remarkable for the facility with which it may be coagulated by the contact of certain animal membranes; thus a piece of 'rennet,' which is nothing else than the dried stomach of a calf, will coagulate the caseine of 1800 times its weight of milk. Further, Caseine appears to surpass albumen in its power of combining with the phosphates of lime and magnesia, and rendering them soluble; and it seems to be in this mode, that the earthy phosphates, which are so important for the consolidation of the bones of the suckling animal, are introduced into its system.—Save in the larger proportion of these substances, the Saline matter of Milk is nearly the same as that of blood.—The Sugar of Milk is peculiar as containing nearly 12 per cent. of water; so that it may really be considered as a hydrate of sugar. It is nearly identical in its composition

with starch; and it appears to be directly formed at the expense of the farinaceous elements of the food. Sugar of milk is chiefly remarkable for its proneness to metamorphosis into lactic acid, under the influence of a decomposing animal membrane which acts as a 'ferment;' and it is thought by some, that the agency of such a membrane in occasioning the coagulation of caseine, is first exerted in producing lactic acid, which in its turn acts upon the caseine.—The Oleaginous globules, which consist of the substance called butyrine, are surrounded by a thin pellicle, that keeps them from coalescing whilst the milk is at rest; but when it is agitated, the envelopes of the oil-globules are broken, and they run-together, so as to form butter. It has been ascertained that butyric acid is one of the products of the change in sugar produced by the contact of putrescent animal membranes; and it can scarcely be doubted that it is directly producible by the transformation of that substance in the living body.—Thus Milk contains the three classes of organic principles, which form the chief part of the ordinary food of animals, namely, the albuminous, the saccharine, and the oleaginous; together with those mineral compounds, which are required for the development and consolidation of the fabric of the infant. It would appear, however, that the proportions of these may vary considerably; having reference partly to the composition of the food on which the animal is habitually supported, and partly to the constitution of the animal itself. Thus, in the Carnivora, so long as they live upon a purely-animal diet, the milk contains little sugar; but if they be fed upon a mixed diet, sugar soon becomes abundant in their milk. Amongst the different species of Herbivorous animals, also, the proportion of the several ingredients varies considerably; and it is also liable to variation in the same individual, according to the nature of the food, the amount of exercise taken by the animal, and other circumstances. Thus in the milk of the Cow, Goat, and Sheep, the average proportions of Caseine, Butter, and Sugar are nearly the same one with another, each amounting to from 3 to 5 per cent. In the milk of the Ass and Mare, on the other hand, the proportion of caseine is under 2 per cent., the oleaginous constituents are scarcely traceable, whilst the sugar and allied substances rise to nearly 9 per cent. In the Human Female, the saccharine and oleaginous elements are both present in large amount; whilst the caseine bears a smaller proportion.—The proportion of the saccharine and oleaginous elements appears to be specially affected by the amount in which these are present in the food, and by the degree in which the quantity ingested is consumed by the respiratory process. Thus, a low external temperature, and out-door exercise, by increasing the production of carbonic acid from the lungs, occasion a consumption of the oleaginous and saccharine matters which might otherwise pass into the milk, and thus diminish the amount of cream. On the other hand, exercise favours the secretion of caseine; which would seem to indicate, that this ingredient is derived from the disintegration of the azotised tissues. Thus in Switzerland, the cattle which pasture in exposed situations, and which are obliged to use a great deal of muscular exertion, yield a very small quantity of butter, but an unusually large proportion of cheese; yet the same cattle, when stall-fed, give a large quantity of butter, and very little cheese.

4. *On the Laws of the Exercise of the Generative Function.*

613. When we contemplate the immense number of diversified forms, which the study of the Organised creation brings under our notice, and witness these distinct forms perpetuated, as it would seem, by the process of Generation, so as to constitute separate races, the question naturally arises, whether all these had a different origin; or whether the characters of any of them have been so modified in the course of time, as to lead to the belief in a diversity of origin among those, which were at first really identical. When it can be *shown* that two races have had a separate origin, they are regarded as of *different species;* and, in the absence of proof, this is *inferred,* when we see some peculiarity of organisation, characteristic of each, so constantly transmitted from parent to offspring, that the one cannot be supposed to have lost, or the other to have acquired it, through any known operation of physical causes. It is, therefore, a point of the utmost importance to the Naturalist, to ascertain what these constant distinctions are; whilst it is an investigation of high interest, in a Physiological point of view, to trace the modifying influence of external circumstances upon the structure and functions of living beings, and to enquire how far the results of such influences may be transmitted hereditarily, so that the differences produced by them may be perpetuated.—Where races which have originally sprung from a common stock present marked differences, they are spoken-of as *varieties;* and the variety may be *transient,* from its peculiarity manifesting a tendency to disappear, or *permanent,* where it continues to be transmitted without change. The uncertainty of the reputed limits of species is daily becoming more and more evident; and every Naturalist is aware, that a very large number of races are usually considered as having distinct origins, when they are nothing more than permanent varieties of a common stock. Whilst the exertions of the enterprising discoverer are adding to our already enormous list of species, from the unexplored resources of foreign lands, the skill of the horticulturist and of the breeder is exerted to produce new varieties of species already in our catalogues; and it has unfortunately too often happened, that a new specific name has been invented for the latter as well as for the former; and that a mere hybrid or transient variety has thus taken the rank of a species, to the confusion of all true principles of arrangement. The philosophic naturalist, on the other hand, aims to reduce the number of species, by investigating the degree of variation which each is liable to undergo, the forms it assumes at different periods of its existence, the permanent characters by which it may be distinguished during its whole life, the habits which are natural to it, the degree in which these may be changed by the influence of circumstances; and, in fine, he endeavours to become acquainted with the *whole* Natural History of a reputed species, before separating it from another to which it may be closely allied.

614. Many examples may be given, of the success with which this mode of investigation is now being prosecuted. The belief which is gaining ground, that many diversified forms of the simpler Cryptogamia, especially Fungi, may arise from similar germs developed under different circumstances, has already been noticed (§ 489); and among the higher Plants, the experiments of Mr. Herbert on the primrose, cowslip, oxslip,

and polyanthus (which he has proved to be all varieties of one species), are sufficient evidence of the important results which would probably accrue from a similar investigation in other quarters. The uncertainty of all principles of arrangement founded upon arbitrary characters, has been demonstrated by the fact recently published,[*] that the flowers and pseudo-bulbs of three reputed *genera* of Orchideous plants have been produced by the same individual.[†]—In Zoology, again, it is only necessary to recall the phenomena which have been arranged under the head of 'alternation of generations,' to see how diverse may be the forms presented by the very same being at different epochs of its existence. The great influence of external circumstances in modifying the form of shells, has been pointed-out by Mr. J. E. Gray;[‡] who has shown, among other instances, that what have been regarded as *six* distinct species of *Murex* are in reality but different states of *one;* and Mr. S. Stutchbury has been equally successful in reducing the number of species of *Patella*, *Cypræa*, and *Oliva*, by attending to the changes of form which each individual undergoes in the progress of its development. Many instances might be related, in proof of the uncertainty of reputed specific distinctions among higher classes; thus, Insects have been seen presenting the characters of different species on the two sides of the body; and it is now certain that an erroneous multiplication of species among Birds, especially in the migrating tribes, has been occasioned by their change of plumage at different seasons.

615. The Naturalist endeavours to simplify the pursuit of his science, by the adoption of easily-recognised external characters, as the basis of his classification of the multitudinous forms which he brings together; but such can only be safely employed, when indicative of peculiarities in internal structure, which are found to be little subject to variation, and which are not liable to be affected by the influence of physical causes. The colour of flowers, for example, is liable to so much alteration from the influence of soil and climate, that it is seldom regarded as of itself any test of the unity or diversity of species. In certain moths and butterflies, on the other hand, the uniform appearance of particular spots on the wings is held sufficient to constitute a specific character, because it is never known to vary in those kinds; and it would probably be found associated, if the examination were pushed far enough, with some unequivocal differences in the configuration of internal organs: in other cases, however, there is considerable tendency to change; but, as in the colouring of plants, there are usually certain limits within which the varieties of shade are restrained. Sometimes one sex varies extremely little, while the form and colour of the other present much diversity. Amidst all these difficulties attending the discrimination of species from structural characters alone, it is not unreasonable to enquire, if there be any other means of effecting the object with greater certainty. This subject has been fully considered by Dr. Prichard in his elaborate work on the Physical History of Man; all that can be here adverted-to, are the

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[*] "Linnæan Transactions," Vol. XVII.

[†] This fact has also come under the Author's own notice in the Durdham Down Nursery, near Bristol, two of the genera being the same as in the instance just quoted, but the third a different one, so that *four* may thus be regarded as of the same species.

[‡] "Philosophical Transactions," 1833.

laws according to which the intermixture of species, and the transmission of hereditary or acquired peculiarities from parent to offspring, appear to take place.—The conclusion which has now been attained on the first of these points, and which (if stated in a sufficiently general form) is equally applicable to both the Animal and Vegetable kingdoms, may be regarded as one of the most valuable tests which the naturalist possesses. In Plants, the stigma of the flower of one species may be fertilized with the pollen of an allied species; and, from the seeds produced, plants of an intermediate character may be raised. But these *hybrid* plants will not usually perpetuate the race; for, although they may ripen the seed for one or two generations, they will seldom continue to reproduce themselves beyond the third or fourth.* But, if the intervention of one of the parent-species be used, its stigma being fertilized by the pollen of the hybrid, or *vice versâ*, a mixed race may be kept-up for some time longer; but it will then have a manifest tendency to return to the form of the parent whose intervention has been employed. Where, on the other hand, the parents were themselves only varieties, the hybrid is only another variety, and its powers of reproduction are rather increased than diminished; so that it may continue to propagate its own race, or may be used for the production of other varieties, almost *ad infinitum*. In this way many beautiful new varieties of garden flowers have been obtained, especially among such species as have a natural tendency to change their aspect.† Amongst Animals, the limits of hybridity are more narrow, since the hybrid is totally unable to continue its race with one of its own kind; and although it may be fertile with one of its parent-species, the progeny will of course be nearer in character to the pure blood, and the race will ultimately merge into it.‡ In Animals, as among Plants, the mixed offsprings originating from different races within the limits of the same species, generally exceed in vigour, and in the tendency to multiply, the parent-races from which they are produced; so as often to gain ground upon the older varieties, and gradually to supersede them. Thus, the mixture of the European races with the Hindoo and South American, has produced tribes of such superior characters of body, and of such rapid tendency to multiplication, that there is reason to believe that they will ultimately become the dominant powers in the community.§ The general principle, then, is that beings of *distinct species*, or descendants from stocks originally different, are not likely to produce a mixed race which shall possess the capability of perpetuating itself; whilst the union of *varieties* has a tendency to produce a race superior in energy and fertility to its parents.

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* The strict form in which this law has been stated in former editions of this work, appears to require modification; Dr. Bell Salter having obtained fertile hybrids between *Epilobium tetragonum* and *E. montanum*, and between *Geum rivale* and *G. urbanum*,—species whose diversity can scarcely be questioned. (See the "Phytologist," Vol. IV., p. 737.)

† There are many instances in which foreign plants, that have been introduced into this country under different specific names, have been found capable of producing fertile hybrids; in these cases a more accurate examination of the original locality has generally shown, that the parents were nothing more than permanent varieties, or even hybrids naturally occurring between other varieties. This is particularly the case with many of the South American genera, such as that elegant garden flower, the *Calceolaria;* and this is probably the explanation of the almost indefinite number of splendid varieties, well known to horticulturists, which may be obtained from the South American *Amaryllis*.

‡ One or two instances have been mentioned, in which a Mule has, from union with a similar animal, produced offspring; but this is certainly the extreme limit, since no one has ever maintained that the race can be continued further than one generation, without admixture with one of the parent-species.

§ Several additional instances of this kind are related in Dr. Prichard's work, Vol. I., p. 147, and in Mr. G. Combe's "Constitution of Man," chapter v.

616. In examining into the characters of the different species of Plants and Animals, with which different regions on the earth's surface are peopled, the Naturalist soon becomes aware that there are many kinds which are restricted to particular localities, whilst others are diffused extensively or even universally over the globe;—that there are some spots (especially insular ones), of which the aboriginal inhabitants are almost entirely different from those elsewhere found;—and yet that amongst these, there will always be found species holding the same rank with regard to the remainder, and thus representing each other in different countries.* Thus, the species of Plants and Animals, originally inhabiting the eastern and western hemispheres, were probably almost entirely different, until the agency of man changed their geographical distribution; and almost the same may be said of the species north and south of the equator. On the other hand, Man, and his constant attendants the dog and the house-fly, exist in every quarter of the globe. Again, we find in New Holland no quadrupeds which do not belong to the order *Marsupialia* or *Monotremata*, with the exception of a dog which is believed to have been introduced by man, and to have run wild; and none of these species are found elsewhere. The greater part of the plants also belong to distinct genera; and those included in the genera occurring elsewhere constitute distinct species,—with scarcely any exception but among the Cryptogamia, the distribution of which seems more extended than that of Flowering-plants. The Flora of insular situations, if at a great distance from land, contains very few species which occur elsewhere. Thus, among the Flowering-plants of St. Helena, which is so far removed even from the western shores of Africa, there have been found, out of 61 native species, only *two* or *three* which exist in any other part of the globe. From these and many similar facts it appears fair to conclude, that every species of plant and animal had originally a distinct centre, from which it has spread itself, according to the capabilities possessed by its structure of adapting itself to changes in its external conditions, its own locomotive powers, and the degree in which it is subject to external agencies. "What is a rare plant," says Decandolle, "but one which is so organised that it can only live in a particular locality, and which perishes in all others; such a plant is incapable of assuming different forms. What, on the other hand, is a common plant? It is one robust enough to exist in very different localities, and under very different circumstances, and which will therefore put on many different forms." Plants, then, are liable to run into varieties, in proportion as they are more robust, more common, or more cultivated; and

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* "We see in two distant countries a similar relation between the Plants and Insects of the same families, though the species of both are different. When Man is the agent in introducing into a country a new species, this relation is often broken; as one instance of this I may mention that the leaves of the cabbages and lettuces, which in England afford food to such a multitude of slugs and caterpillars, in the gardens near Rio are untouched." Darwin, in "Journal of the Voyage of the Beagle."

some native species are, from this cause, domesticated with greater difficulty than many exotics. Precisely the same may be said of Animals; those which have the power of adaptation to differences of temperature, food, &c. are most universally diffused; while those that can only exist within narrower limits of variation, are restricted to the neighbourhood of their original locality.*

617. It becomes a most interesting question, then, to determine what are the changes which may be produced by the influence of external circumstances, and how far these are hereditarily transmissible. On this subject, a few facts may be stated, which will give an insight into the nature of the enquiry; but it is one which deserves more attention than it has yet received, since it is not only essential to the correctness of all Natural-history classifications, but is connected with some of the highest questions in Physiological science.—One of the most obvious distinctions, where it is well-marked, is that of *size;* and yet, as we have already seen (§ 118), it is one peculiarly open to fallacy. Not only the size of the entire organism, but the relative development of individual parts, may be greatly modified by the supply of food; this is especially the case in Plants, whose tissues are simple, and whose different organs closely resemble each other in elementary constitution. Thus, cultivation not only converts a 'single' flower into a 'double' one (§ 92), but obliterates spines, prickles, and thorns, from the surface of many plants; a change which was fancifully, but not improperly, termed by Linnæus "the taming of wild fruits." The instances of such alterations effected by external agency in the Vegetable kingdom, are almost innumerable; and they are not confined to structure, being observed in habit also. Thus, many plants, which are *annuals* in a cold climate, become *perennial* if transported to the torrid zone; and plants which are usually *biennial,* forming their organs of vegetation one year, and those of fructification in the second, and then perishing, may be converted into *annuals* by heat, or into *triennials* by cold. It is very difficult, however, to say how far the varieties thus created may become permanent by their hereditary transmission. The usual principle is, that propagation by seeds will only reproduce the *species,* the *race* not being continued with any certainty. In most Plants which have been much altered by cultivation—such as the Apple, the Cabbage, or the Dahlia—the seeds, if dropped on a poor soil, will produce offspring which approximates to the original type of the species; whilst from the seeds of the *Cerealia* (corn-grains), which are believed to have been originally grasses of some very different aspect, no other forms are ever produced, which might assist in the solution of the curious problem of their origin. It is not improbable that, as among animals, varieties which arise from some peculiarity in the constitution of the being itself, are more liable to be reproduced in the offspring, than those which are simply the result of external agencies. It is evident, at least, that here also the capability of undergoing such modifications, is that which renders the species most truly valuable to Man.

618. Amongst Animals, the various breeds of domestic cattle, of the

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* The geographical distribution of organised beings is a question of the highest interest to the Physiologist as well as to the Naturalist; and it is one of those which requires the utmost elucidation it can obtain from the combined researches of both. It is a department of inquiry which is at present being most successfully prosecuted by Prof. E. Forbes.

horse, dog, &c. afford abundant evidence of the modifying influence of external conditions; since there is little doubt that they have respectively originated from single stocks, and that their peculiarities have been engrafted, as it were, upon their specific characters. Between the Shetland pony and the Arabian racer, for example, or between the Newfoundland dog and the Italian greyhound, there would seem much greater difference than between the Lion and Tiger (the skulls of which are so much alike that even Cuvier was not always able to distinguish them), or between various other species of the Feline tribe, which, from the incapability of domestication, have not been exposed to such influences. But that these domesticated races, however different their external characters, have a common origin, is indicated by the perfect freedom with which they breed together; and by the fact that, whenever they return to a state of nature,—as is the case with the dogs introduced by the Spaniards into Cuba, and the horses and wild cattle which now overspread the plains of South America,—the differences of breed disappear, and a common form is possessed by all the individuals. It is not a little curious, too, that instincts which must have remained dormant for many generations during the domesticated condition of the race, should re-appear when this change takes place in its habits; thus, among the wild horses of South America, there is the same tendency to associate in herds, under the protection of a leader, as among those of Asia, whose ancestors are not known to have been ever reduced to subjection. "It seems reasonable to conclude," as Sir C. Lyell has justly remarked, "that the power bestowed on the horse, the dog, the ox, the sheep, the cat, and many species of domestic fowls, of supporting almost every climate, was given expressly to enable them to follow man throughout all parts of the globe, in order that he may obtain their services, and they our protection." "Unless some animals had manifested in a wild state an aptitude to second the efforts of man, their domestication would never have been attempted. If they had all resembled the wolf, the fox, and the hyæna, the patience of the experimentalist would have been exhausted by innumerable failures, before he at last succeeded in obtaining some imperfect results; so, if the first advantages derived from the cultivation of plants, had been elicited by as tedious and costly a process as that by which we now make some slight additional improvement in certain races, we should have remained to this day in ignorance of the greater number of their useful qualities."

619. How all those varieties have been produced, which are now so numerous and striking, is a question much more easily asked than replied to satisfactorily. That very important changes may be induced by the direct influence of climate, food, and habits of life, upon successive generations, cannot be doubted; since experience shows that particular races of animals, placed under new conditions, gradually undergo modifications which adapt them to those conditions. Thus, of the number of new varieties which have sprung-up amongst the domesticated races first introduced into South America by the Spaniards, there are many which are clearly traceable to climatic influences; and even within a recent period, numerous examples of a similar modification have occurred. For example, Sir C. Lyell mentions that some Englishmen engaged in conducting the operations of the Real del Monte Company in Mexico, carried-out

with them some greyhounds of the best breed, to hunt the hares which abound in that country. The great platform which is the scene of sport, is at an elevation of about 9000 feet above the level of the sea, and the mercury in the barometer stands habitually at the height of about 19 inches. It was found that the greyhounds could not support the fatigues of a long chase in this attenuated atmosphere; and before they could come-up with their prey, they lay down gasping for breath; but these same animals have produced whelps, which have grown-up, and are not in the least degree incommoded by the want of density in the air, but run-down the hares with as much ease as do the fleetest of their race in this country.—But peculiarities sometimes arise, to all appearance *de novo*, which cannot be attributed with the same degree of probability to external agencies; thus, it is by no means uncommon to find individuals of the Human species with six fingers and six toes; and such peculiarities are more likely to be continued hereditarily, than are those which have been acquired. Advantage has been sometimes taken by Man, of spontaneous variations of this kind, for some purpose useful to him; and he has exerted his skill to perpetuate them. The following example is of comparatively recent occurrence. In the year 1791, one of the ewes on the farm of Seth Wright in the state of Massachusets, produced a male lamb, which, from the singular length of its body and the shortness of its legs, received the name of the *otter* breed. This physical conformation, incapacitating the animal from leaping fences, appeared to the farmers around so desirable, that they wished it continued. Wright determined on breeding from this ram, and the first year obtained only two with the same peculiarities; in the following years, he obtained greater numbers; and, when the offspring became capable of breeding one with another, a new and strongly-marked variety, before unknown to the world, was established.*—This history shows the influence which the circumstance of a scanty population may have formerly had on the production of varieties, both in the human and other species. At the present time, any peculiarity which may occasionally arise, speedily merges by intermixture, and returns to the common standard; but it may be surmised that, in the older ages of the world, some individuals in which a peculiarity existed, may have been so far separated from the rest, as to necessitate frequent union among themselves, so that the character would be rendered still more marked, instead of disappearing; and, being propagated for a few generations, would be rendered permanent.

620. Acquired peculiarities, on the other hand, are seldom reproduced in the offspring, unless they have a relation with the natural habits and physical wants of the species; but, when this relation exists, they may be transmitted as regularly as the specific characters. Thus, in Dogs, the relative perfection of the organs of sight and smell, perhaps also of hearing, varies much in different breeds, and their mode of hunting their prey undergoes a corresponding change; but in these cases, no new instinct is developed, the difference merely consisting in the relative

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* "Philosophical Transactions," 1813.—A very similar account has been recently given by Prof. Owen (in a lecture delivered before the Society of Arts, Dec. 10, 1851), respecting the introduction of a new breed of Merino Sheep, distinguished for the long, smooth, straight, and silky character of the wool, and now known as the 'Mauchamp breed.'

proportion of those already existing; and the new peculiarities have an intimate relation to the habits of the animal in a wild state. For example, in a mongrel race of dogs employed by the inhabitants of the banks of the Magdalena almost exclusively in hunting the white-lipped Pecari, a peculiar instinct appears to have become hereditary, like that of the pointers and other dogs of this country. The address of these dogs consists in restraining their ardour, and attaching themselves to no animal in particular, but keeping the whole herd in check. Now among these dogs some are found, which, the very first time they are taken to the woods, are acquainted with this mode of attack; whereas, a dog of another breed starts forward at once, is surrounded by the Pecari, and, whatever may be its strength, is destroyed in a moment.*—It is impossible not to recognise in many acquired habits, however, something more than a relation to the instincts necessary for the preservation of the species; they evidently arise, in part at least, from the connection of the race with Man. This is more particularly exemplified in the instance of the breed of Shepherd's Dogs, which often display an extraordinary hereditary sagacity respecting their peculiar vocation; as well as in cases which have been frequently mentioned, where the descendants of dogs to which peculiar tricks have been taught, have displayed an unusual aptitude for learning the same. It may then be considered, that the capability of undergoing such modifications is a part of the psychical as well as structural character of the Dog, even in a wild state; and that his relation to Man may have as important an influence on *his* hereditary propensities, as the supply of their physical wants has on animals of other species. The same may, perhaps, be said of the Horse, in the races of which we find peculiar habits transmitted from parent to offspring, which are the pure results of human instruction.—It is from the want of this relation towards either the natural habits of the species or their subserviency to man, that habits acquired by other animals do not become hereditary. Thus, although Pigs have been taught to hunt and point game with great activity and steadiness, and other learned individuals of the same species have been taught to spell, these acquirements have in no instance been transmitted to the offspring, not being the result of the development or modification of any instinctive propensity naturally existing. In like manner, however artificially the forms of domesticated animals may have been altered in all the individuals of successive generations, the usual character of the species and variety is maintained in each one of the offspring; unless, as sometimes occurs, this alteration happens to coincide with natural varieties of the species. Thus instances are on record, in which Dogs, that have been deprived of their tails by accident or design, have produced puppies with a similar deficiency; but as breeds of tail-less dogs have spontaneously arisen, there would be a stronger tendency to the perpetuation of this acquired peculiarity, than when no such peculiarity naturally occurred. There can be no doubt that much has yet to be learned, of the influence of the mental state of the parent upon the development of the offspring; and that, though credulity and the love of the marvellous have been the occasion of many strange fictions being

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[*] Some curious instances of a similar propagation of acquired peculiarities connected with the natural habits of the race, are given by Mr. Knight, "Phil. Trans." 1837; the most remarkable, perhaps, are the facts related of the Retriever.

transmitted to us, we are by no means justified in rejecting the doctrine without further enquiry. And when it is borne in mind, that the races of animals among which the so-called *spontaneous* variations are most apt to spring-up, are also those which are most susceptible of the modifying influence of external conditions, it seems highly probable that these spontaneous variations in the offspring are really attributable to the influence of external agencies in modifying the constitution of the parent. Of this view we have an interesting illustration in the fact mentioned by Mr. T. Bell, that the first litter of puppies produced by an Australian *dingo* in confinement and in a half-domesticated state, were all more or less spotted; although both parents were of the uniform reddish-brown colour which belongs to the race, and the mother had never bred before.*

CHAPTER XII.

OF THE SENSIBLE MOTIONS OF LIVING BEINGS.

621. ALTHOUGH we are ordinarily accustomed to think of Animals as self-moving, and to regard Plants as altogether destitute of the power of spontaneous motion, yet, as already pointed out on several occasions, this distinction between the two kingdoms is one of which the validity cannot be sustained. For the 'zoospores' of many of the inferior Algæ are as active in their movements, as are the Animalcules which they so much resemble; and there are some Protophytes, which seem to be in a state of more or less active motion during the whole period of their lives, at least until the occurrence of 'conjugation.' Thus the *Oscillatoriæ*, which are long filamentous cells, have a movement of alternate flexion and extension, writhing like worms in pain; sometimes they appear to twist spirally, and then to project themselves forwards by straightening again. These movements are greatly influenced by temperature and light, being more active in heat and sunshine than at a low temperature and in shade; and they are checked by any strong chemical agents, which also put a stop to the motions of Animalcules inhabiting the same water. Most of the *Diatomaceæ*, also, move slowly through the water, as if by the action of cilia; although these organs are not distinctly discernible.† Among the higher Algæ, and probably in the whole Cryptogamic series, the 'antherozoids' possess an activity in no degree inferior to that of the spermatozoa of Animals. And although the different mode in which the generative function is performed in the Phanerogamia, renders it unnecessary that the contents of the sperm-cells should possess such a power of spontaneous

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* "British Quadrupeds," 2nd Edit., p. 203. See also Montgomery, "On the Signs of Pregnancy," p. 16, Walker "On Intermarriage," pp. 275—8, and Dr. Harvey "On a remarkable Case of Cross-breeding," for several examples of the influence of the mental condition of the mother at the time of conception, upon the offspring.

† The *Bacillaria paradoxa* has a very remarkable movement; for the long staff-like frustules of which the plant is composed, slide edgeways over one another until they become almost completely detached, and then return and slide in the opposite direction; repeating this movement with a rhythmical regularity.

movement, and the entire organisms are firmly rooted to the ground during the whole of life, yet we shall hereafter find that they exhibit movements of one part upon another, which are scarcely inferior in character to those of Zoophytes,—these also being fixed during the greater part of their existence, although its earliest period has been passed by them in a condition resembling that of the zoospores of the inferior Algæ.

622. Now with regard to *ciliary* movements, it may be asserted without hesitation that they do not in the least indicate consciousness or self-determining power on the part of the beings which exhibit them; and there is no reason whatever, why the fact of their performance by any organism should be regarded as entitling it to a place in the Animal kingdom. It cannot, indeed, but induce us to look at those movements of Animalcules, which are due to ciliary action, as of a purely-automatic character, to see that movements of a precisely-similar nature are performed by beings whose place is indubitably in the Vegetable kingdom. In fact, there seems no other line of demarcation to be drawn between the Protophyta and Protozoa, than that which is based upon the nature of their respective aliments, and the mode in which these are obtained and appropriated.—And the same may be said of those rhythmical motions which are exhibited by *Oscillatoriæ*, and by 'antherozoids' and 'spermatozoa;' their very uniformity and constancy being indications that they do not proceed from a self-determining power, but are entirely automatic. Such movements, appear to result from the expenditure of a certain amount of Vital force, which becomes reconverted into the Physical, through the peculiarity of the material structure which is its instrument. (See GENERAL PHYSIOLOGY.)

623. The sensible motions of the higher Plants, however, which are usually performed under the influence of stimuli applied to their tissues, or to certain parts of them, appear referable to a somewhat different category; being, in fact, manifestations of the same property of *contractility*, as that which exists in certain Animal tissues, but especially in the muscular. This property of *contractility* on the application of a stimulus, may be readily distinguished from the *elasticity* which is simply due to the mechanical relation of the particles composing the tissue; the latter being retained as long as there is no evident decomposition, whilst the former is an essentially *vital* endowment. An elastic ligament, when stretched, tends to contract only in virtue of that disturbance of its molecular arrangement, which has been produced by the force applied to it; but a muscle which contracts powerfully upon the stimulus of a simple touch, or upon one of a still less mechanical nature, can do so only by a property of its own, which is connected with its attributes as a living being. In the lowest and simplest Animals, whatever degree of contractility is possessed, appears to be almost equally diffused through the system (§§ 35, 37); and we can neither discover in them any structure specially endowed with this property, nor discern anything resembling a nervous system fitted to call it into exercise. In proportion as we ascend the scale, however, we find a distinct Muscular structure evolved, in which the general contractility of the body becomes, as it were, concentrated; and, in proportion to its development and complexity, it supersedes the corresponding but more feeble powers of the remainder of the tissues. It is now in great degree subjected to the Nervous System; and

all those parts of it, which are not connected with the functions of Organic life merely, are rendered subservient to the Will, and thus become the instruments of its operation upon the place and condition of the body.

624. Of the evident movements observable in the higher Plants, there are some which take place as a part of the regular series of phenomena of growth and reproduction, and which must be regarded as the ordinary expressions of the vital forces which they have derived from the light, heat, &c. that have sustained their organic activity; but there are others which are performed in respondence to excitement of a mechanical kind. The immediate connection of these movements with the organic functions, in the first class of instances, and the indication they would seem to give of consciousness and sensibility in the second, have led many persons to seek for an explanation of them, in the hypothesis of the existence of a nervous system in these beings. But it will be seen, if the question be fairly investigated, that, whilst no evidence of its presence is furnished by the minutest anatomical research, no argument for its operation can be deduced from the phenomena observed.—In the simplest and most intelligible instances of sensible motions in Plants, the change is the result of the contraction of the part to which the stimulus is applied; this contraction being consequent upon the change of form of its cells, which must be regarded as a manifestation of their peculiar vital endowments. Thus, the leaf of the wild Lettuce exudes, when the plant is in flower, the milky juice contained in its vesicles, if these be irritated by the touch; and the contraction of the poison-gland of the Nettle, when the tubular hair which surmounts it is pressed, forces-out its secretion, and produces urtication. So, again, if the base of the filament of the Berberry be touched with the point of a pin, the stamen immediately bends-over and touches the style. In this case, the movement is produced by the peculiar contractility of the tissue on the interior side of the filament, which, when called into operation by the application of a stimulus, necessarily occasions the flexion of the stalk. This peculiar irritability has a relation with the functions of the flower; since, when called into play (as it frequently is) by the contact of insects, the fertilization of the stigma will be assisted. Many similar instances might be adduced, in which a corresponding operation is connected with the process of reproduction in plants. —There are cases of more complexity, however, in which an irritation in one part produces motion in a distant and apparently-unconnected organ. Thus, in the *Dionæa muscipula* (Venus' fly-trap), the contact of any substance with one of the three prickles which stand upon each lobe of the leaf, will occasion the closure of the lobes together, by a change taking place in the leaf-stalk. And in the *Mimosa pudica* (Sensitive plant), any irritation applied to one of the leaflets will occasion, not only its own movement towards its fellow, but the depression of the rib from which it springs; and, if the plant be healthy, a similar depression will be produced in the principal leaf-stalk, and even in the petioles of other leaves. This propagation of the effect of the stimulus, from one part, to another more or less remote, is usually accomplished in Animals through the nervous system; but there is little doubt that in plants the transmission is made through an entirely different channel. For the experiments of Dutrochet upon the Mimosa have shown it to be through the vascular system, that an irritation in one part is made to produce movement in a

distant organ; and there can be little doubt that the same is true of the Dionæa also. Where each leaflet of the Mimosa is implanted upon its rib, there is a little swelling or intumescence; this is more evident where the lateral ribs join the central one; and it is of considerable size at the base of the petiole, where it is articulated with the stem. The experiments which have been made upon its properties, have been performed, therefore, in the latter situation; but the description of their results will apply equally well to the rest. The intumescence consists of a succulent tissue, which, on the upper side, appears very distensible, and on the lower very irritable. In the usual position of the leaf or leaflet, the distension of the two sides seems equally balanced; but anything which causes an increase of fluid on the upper side, or a contraction of the vesicles on the lower, will obviously give rise to flexion of the stalk. The latter effect may be readily produced by touching that part of the intumescence itself; and then the leaf or leaflet will be depressed by the contraction of the part *immediately* irritated, just as in the case of the stamen of the Berberry. The same result follows the stimulation of this part by an electric spark, by the concentration of the sun's rays upon it with a burning glass, or by chemical agents; and if, instead of applying a temporary stimulus, whose effect is speedily recovered-from, a notch be made in the lower side of the intumescence, the balance between its resistance and the expansive tendency of the upper side is then permanently destroyed, and the stalk remains depressed. Now, supposing the lower side to be in its usual condition, flexion of the stalk may result also from whatever distends the vesicles of the upper part of the intumescence; and this is the mode in which the movement is usually effected. For a stimulus applied to any part of the leaf, will cause a contraction of its vesicles; and the fluid expelled from them is carried by the circulating system to the distensible portion of the intumescence belonging to each leaflet, and to that of the petiole itself.—It appears, then, that these evident motions are readily explicable on the supposition, that *contractility* is a property of various tissues of Plants, and that this may be excited by stimuli of a physical nature. To suppose more, would be unphilosophical because unnecessary.

625. There are other movements, however, arising from causes which originate in the system itself, of which some notice should be taken. Such are, the folding of the flowers and drooping of the leaves, known as the *sleep* of plants. These phenomena seem due to a diminution in the activity of those vital processes, by which the turgescence of the soft parts of the structure is maintained; and this diminution appears partly to result from the withdrawal of the usual stimuli, especially Light, and to be in part of a periodical character. For it is found that artificial light and warmth will cause many flowers and leaves to erect themselves for a time; and that, by proper management, the usual periods may be completely reversed. But the phenomenon cannot be altogether explained on this principle, since there are many plants of which the flowers only expand in the night, and which must be kept in darkness to prevent them from closing; and in the present state of our knowledge, we can only consider this *periodicity*, like that periodical cessation or augmentation of particular functions which is common to nearly all organised beings, as a part of that regular train of operations, which is characteristic of each living being, and which proceeds from the original endowments of its organism,

called into exercise by forces external to itself.—One other spontaneous Vegetable motion may be instanced, as of a very inexplicable character; that of the *Hedysarum gyrans*, a Bengalese plant, each of whose petioles supports three leaflets, of which the central one is large and broad, and the two lateral ones, which are situated opposite to each other, small and narrow. The position of the central leaflet is peculiarly influenced by light: for in the day-time the leaflet is usually horizontal; by the action of strong solar light it is raised towards the stalk, whilst in the evening it bends downwards; and it is manifestly depressed, if placed in the shade for a few minutes only. The small lateral leaves are in incessant motion; they describe an arch forwards towards the middle leaflet, and then another backwards towards the footstalk; and this by revolving on their articulation with the petiole. They pass over the space in 30 or 40 seconds, and then remain quiet for nearly a minute; the leaflets do not move together, but in opposite directions, one usually rising while the other is sinking; the inflexion downwards is generally performed more rapidly and uniformly than that upwards, which occasionally takes place by starts. These movements continue night and day; being slower, however, in cold nights, and more rapid in warm and moist weather. They seem less affected by mechanical or chemical stimuli, than do those of any other plant; and continue for a longer time in separated parts.

626. One class of spontaneous Vegetable movements has been shown by Dutrochet to be due to an act of Endosmose (§ 169) in the organs which execute them. This is particularly the case in various seed-vessels, which burst when ripe, in such a manner as to eject their contents with force,—as in the instance of the *Momordica elaterium* (common Squirting-Cucumber). His experiments upon the capsule of the Balsam termed *Impatiens noli-me-tangere* are particularly interesting. The valves of this capsule, when the fruit is ripe, suddenly spring from each other and curl inwards, scattering the seeds to some distance. Now an examination of the tissue of the valves shows, that the outer part consists of much larger vesicles than the inner; and that the fluids contained in it are the densest. According to the law of Endosmose, the fluids contained in the tissue of the interior will have a tendency to pass into the vesicles of the exterior; and it will distend them in such a manner, as to produce a disposition in that side to expand, when permitted to do so, whilst the inner side has an equal disposition to contract. This at last occurs from the separation of their edges consequent upon their ripening; and then each valve rolls inwards. If, however, the valves be placed in a fluid more dense than that contained in the exterior vesicles, such as syrup, or gum-water, these will be emptied on the same principle, and the valves will become straight, or even curl outwards.—A very curious movement, which probably depends upon a similar cause, may be observed in a little Fungus, which is not uncommon in some parts of Britain, named *Carpobolus*, from its peculiar manner of scattering its fruit. The sporules are collected into one mass, and inclosed in a globular bag, which is called a *sporangium*. This lies in a cavity, of which the inner wall is capable of separating itself from the outer, and of suddenly everting itself, so as to project in a globular form from the mouth of the cavity which it previously lined. This sudden eversion ejects the sporangium (with a degree of violence, which for so minute a plant is very remarkable,) from the cavity in which it was formed;

the mouth of this, which was at first nearly closed, spontaneously dilating itself as the sporules are mature. The eversion of the membrane is probably due to a change having taken place in the relative distension of the cells forming its inner and outer layer, which would operate much as in the capsule of the Balsam.

627. Among the simplest *Protozoa*, it seems as if the change of form of the single cell of which each individual is composed, were the sole means of movement which it possesses (§ 139); and this change of form appears often to be due rather to operations taking place *within* the cell, than to occur in respondence to mechanical irritation applied to its exterior,—a circumstance which throws some light upon the phenomena just now described as occurring in Plants (§ 625). In these movements it is impossible to imagine with any probability that consciousness can participate; nor can it be supposed that a nervous system can be their instrument. Now although the movements of the *Hydra* and of other Zoophytes of its class, may *appear* to indicate the existence of a self-determining power, yet it is very doubtful whether such an endowment can be justly assigned to these animals. For their contractile tissue is of the simplest possible character, resembling that which is found in a very early state of newly-forming parts of higher Animals; and the most careful scrutiny has failed to discover the faintest vestiges of a Nervous System in them, notwithstanding that the extreme transparency of their bodies renders them peculiarly favourable subjects for the most minute examination. And further, when their movements are fairly compared with those of higher animals, it becomes obvious that they resemble those by which food is immediately introduced into the stomach, the tentacula of the Hydra being homologous with the œsophageal muscles of Man; and as we know that the latter act without our will, and even without our consciousness, it would be inconsistent with sound philosophy to regard them as dependent upon such springs of action in the Hydra, without some very cogent evidence that they are so.—Again, the rhythmical movements of the disc of the *Pulmograde Acalephæ*, whereby they are propelled through the water, bear a much closer resemblance to the rhythmical contractions of the heart of higher animals, than they do to any other of their actions; and as the latter are performed without any exercise of will, and even without the guidance of consciousness, it seems reasonable to suppose that the former are so likewise. And such an interpretation is confirmed by what is known of the nervous system of these animals; for its extent of diffusion is so limited, that it is impossible to imagine the whole contractile tissue of the disc to be influenced by it; and, moreover, portions of the disc entirely separated from the rest, and not containing any portion of the nervous centres, will continue their alternating contractions and relaxations, just like the heart of a cold-blooded animal taken out of its body.—In the young of the *Compound Ascidians* (§ 558), again, we find an active movement of the embryonic mass through the water, effected by the lateral undulations of the tadpole-like tail; and this at a time when that organ consists of nothing but cells, and when it is certain that the formation of the nervous system has not even commenced. Such movements are strictly comparable, on the one hand, with the rhythmical movements of the Oscillatoriæ or the Hedysarum among Plants, and on the other, with the rhythmical contractions of the heart

in the embryo of the higher Animals, when as yet its walls consist of untransformed cells (§ 255). They cannot be attributed to any external stimulation, and must be regarded as a part of the regular series of vital operations of the cells which exhibit them, as the ciliary vibrations are of the ciliated epithelium-cells, or as the acts of secretion or reproduction are of the cells of glands or ovaries.

628. There are many movements in higher Animals, which, though performed by the instrumentality of the Muscular tissue, are perfectly involuntary, take place without exciting any consciousness of their occurrence, and appear to be essentially independent of Nervous agency, although capable of being affected by it. All the actions of this class are *immediately* subservient to the maintenance of the Organic functions: thus we find the propulsion of food along the alimentary canal to be effected by the peristaltic contractions, alternating with relaxations, of its proper muscular coat; and the circulation of the blood to depend in great measure upon the alternating contractions and relaxations of the muscular walls of the heart. Between these two sets of actions, however, there is this important difference;—that whilst the former, like the closure of the fly-trap of the Dionæa, or the bending-down of the filaments of the Berberry, are chiefly dependent upon the application of a stimulus, which calls into activity the contractile power of the tissues,—the latter, like the rhythmical movements of Plants previously referred-to, take place without any external stimulation, the regular alternation of contraction and relaxation being apparently *their* peculiar manifestation of vital activity. Thus we find that the peristaltic movements of the alimentary canal are for the most part excited by the contact of solid or liquid substances with its lining membrane; and that, when they are not otherwise taking place, they may be called into activity by a slight mechanical irritation applied to its external surface, or, in a warm-blooded animal at least, by the admission of cold air into the abdominal cavity. On the other hand, the alternate contractions and relaxations of the heart will continue with extraordinary regularity (in a cold-blooded animal), after the organ has been removed from the body, and has been completely drained of its blood;* and it seems impossible to refer them to the agency of any stimulation derived from an external source. But, on the other hand, the peristaltic movements of the alimentary canal may be often seen to take place without any ostensible stimulation; and the alternating movements of the heart, after they have ceased, may often be re-excited by a slight mechanical irritation. Hence it is obvious, that both kinds of action are referable to the same endowment; namely, a *motility* which is inherent in the tissues, and is a part of their vital endowments, and which may manifest itself either *spontaneously*, or *in respondence to a stimulus:* but that the former method is the rule in the case of the heart, the exception in that of the alimentary canal; whilst the latter method is the rule in the case of the alimentary canal, the exception in that of the heart.—The endowment in question, however, is not limited in the higher animals to the heart and alimentary canal; for it pervades, in a greater or less degree, the walls of their blood-vessels and absorbents,

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* It has been stated by Dr. Mitchell of Philadelphia, that the heart of a Sturgeon which had been cut-out and hung-up to dry, continued its rhythmical movements, until its tissues had lost so much of their fluid, that a crackling sound was heard with each contraction.

those of the principal gland-ducts, those of the urinary bladder, uterus, &c., all of which parts are furnished with non-striated muscular fibres, composed of those elongated contractile cells, which have been recently shown by Prof. Kölliker to take a considerable share in the movements of the contractile tissues of even the highest animals.*

629. By far the larger proportion of the sensible movements of higher Animals, however, are called-forth by the instrumentality of the Nervous System; through which the contractility of the Muscular apparatus is brought into exercise. This is the case, not only with all those actions that are designated as *voluntary*, being the result of an individual self-determining power, but also with many that are as *involuntary* or *automatic* as are those which we have been just considering; these last being connected, more or less directly, with the maintenance of the Organic functions, or, in some mode or other, with the conservation of the bodily fabric. We shall find that these are performed with no more dependence on consciousness, than the rhythmical contractions of the heart, or the peristaltic movements of the alimentary canal; and that the nervous system is made to participate in them simply as a *conductor* of stimuli, from the parts which receive the impressions, to those which are to respond to them by contraction; the conditions of Animal existence requiring that this conduction shall be performed with greater rapidity and energy, than we see to take place in the parallel cases that present themselves among Plants (§ 624).—It is very interesting, however, to observe, that the form of Muscular tissue which most readily obeys the stimulus of innervation, and which is the instrument of the most purely Animal functions, is that which most perfectly exhibits that *cellular* type of structure, which seems common to all the parts most actively engaged in the vital operations; and that the act of muscular contraction in the highest Animal is due to the same kind of change in the form of the cells of the ultimate fibrillæ, as that which produces the sensible motions of Plants. (See GENERAL PHYSIOLOGY.) The only essential difference, then, between the contractile tissues of Plants and those of the higher Animals, consists in this; that the latter are capable of being called into activity by a kind of stimulus—the Nerve-force—which does not operate in the former. But this speciality of endowment does not supersede the more general susceptibility which exists among the inferior grades; for we find that the 'striated muscular fibre,' although called into action more readily and powerfully by the stimulus of Innervation than by any other, is yet induced to change its state, like the contractile tissues of Plants, by electrical, chemical, or mechanical irritation; whilst the 'non-striated fibre' responds so much more readily to this kind of irritation, than it does to the stimulus of Innervation, that it is even difficult to demonstrate the action of the latter upon it.—To enter into any detail as to the various mechanical adaptations, by which the force generated by Muscular contraction is applied to the production of the movements which are characteristic of the different tribes of Animals, would carry us far beyond the limits of the present Treatise.

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* See "Siebold and Kölliker's Zeitschrift," Band I., 1849.

CHAPTER XIII.

OF THE FUNCTIONS OF THE NERVOUS SYSTEM.

1. *General Considerations.*

630. We have now completed our survey of the entire series of those operations, which are common to the Vegetable and Animal kingdoms; and it only remains for us to consider those which are peculiar to the latter. Such are the various actions of the Nervous System,—an apparatus to which we find nothing in the least analogous among Plants; and the possession of which, therefore, must be considered as the peculiar and characteristic endowment of the Animal. Still, as already pointed-out on several occasions, we cannot justly regard it as universally present throughout those classes, which possess on other grounds a title to be ranked in the Animal kingdom; for there are many such beings, in which we seem entitled to affirm that it is absent; and there are many others, in which, if present at all, it exists in a condition quite rudimentary, and can take little share in the actions of the organism. But the life of all such beings is chiefly *vegetative* in its nature; their movements are not dissimilar in kind to those which we see in Plants; and their title to a place in the Animal kingdom chiefly rests upon the nature of their food, the mode in which they appropriate it, and their resemblance to the embryonic conditions of beings undoubtedly belonging to that group. In proportion, however, as we ascend the Animal series, do we find the Nervous System presenting more and more of structural complication, and obviously acquiring more and more of functional importance; so that in Vertebrated animals, and more especially in Man, it obviously becomes that part of the organism, to whose welfare everything else is rendered subordinate. And we observe that this is the case, not merely in virtue of its direct instrumentality as the organ of Mind; but also as the medium through which the conditions are provided, for carrying-on many of the Organic functions, which we find to be brought into more and more intimate dependence upon it, in proportion as we rise in the scale. Thus the Ingestion of food, and the Aeration of the circulating fluid, which are provided-for in many of the lower tribes of animals by ciliary action (in which Nervous agency has no participation whatever), are made to depend in the higher upon the Nervo-muscular apparatus, which, without interfering with those organic processes that take place (so to speak) in the *penetralia* of the system, guards the *portals* of entrance and exit. But we find that, when thus brought into intimate relation with the Organic functions, the Nervous system is employed in its very simplest mode of operation,—that which does not involve Intelligence, Will, or even Instinct, (in the proper sense of that term), but which may take place independently of all Consciousness, by the simple *reflexion* of an impression, conveyed *to* a ganglionic centre by one set of fibres proceeding towards it from the periphery, along another set which

passes *from* it to the muscles, and calls them into operation. This lowest kind of 'reflex' action, therefore, by which 'automatic' movement is excited without the necessary participation even of consciousness, is the simplest application of the Nervous System in the Animal body. We shall presently see reason to believe, that a very large proportion of the movements of many of the lower animals are of this character; and that they are not necessarily accompanied by sensation, although this may usually be aroused by the same cause which produces them. As we rise, however, in the scale of Animal existence, we find the movements of this class forming a smaller and smaller proportion of the whole; until, in Man, they constitute so limited a part of that entire series of operations of which the Nervous system is the instrument, that their very existence has been overlooked.

631. But the main purpose of the Nervous System is to serve as the instrument of those *Psychical** powers, which are altogether peculiar to the animal. Now when we attempt to analyse these attributes, we may resolve them, like the properties of the material body, into different groups. We find that the *first* excitement of all mental changes, whether these involve the action of the *feelings* or of the *reason*, depends upon *sensations;* which are produced by impressions made upon the nerves of certain parts of the body, and conveyed by these to a particular ganglionic centre, which is termed the *sensorium*, being the part in which Sensation, or the capability of *feeling* external impressions, especially resides. Now there are numerous actions, especially among the lower Animals, which seem to require sensation for their excitement, and which are yet as far removed from the influence of the Will, as little directed by Intelligence, and hence as truly 'automatic' in their nature, as the 'reflex' movements already noticed; these must be attributed to a 'reflex' action on the part of the Sensorial centres. The movement seems, in some instances, to be as immediately consequent upon the production of the sensation, as is the act of sneezing, or the sudden start produced by a loud and unexpected sound, in ourselves. But in other instances it appears rather to proceed from a psychical impulse excited by the sensation; which without any calculation of consequences, any intentional adaptation of means to ends, any exertion of the reason, or any employment of a discriminating Will, may produce an action, or train of actions, no less directly and obviously adapted to the well-being of the individual, than are those whose mechanism has been already described. It is impossible to say, in regard to many of the actions of the lower animals, to what extent they involve feelings or emotions at all analogous to those which *we* experience: and it would seem better to apply the generic term *Consensual* to those, in which the Sensation excites the motor action, either immediately, or through the agency of an indiscriminating impulse excited by the sensation. This class will include all the purely 'instinctive' actions of the lower Animals; which make-up, with those of the preceding group, the whole of the Animal functions in many tribes, and which are peculiarly elaborate in their character, and wonderful in their results, in the class of Insects. It is obvious that such actions, not being the result of any intelligent choice or voluntary direction on the part of the animals which perform them,

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* This term is used to designate the sensorial and mental endowments of Animals, in the most comprehensive acceptation of those terms.

are not less truly 'automatic' than those belonging to the first-named group; the only essential difference being, that the latter are performed without any necessary participation of sensation, the excitement of which appears to be essential to the performance of the latter.—The Automatic movements are found to be gradually subordinated to the Intelligence and Will, as we rise towards Man, in whom those faculties are most strongly developed; their purpose being limited to the maintenance of the Organic functions, in subservience to the more elevated purposes of his existence.

632. Sensations, however, do not always thus immediately give rise to muscular movements; their operation among higher Animals, being rather that of stimulating to action the Intellectual powers. There can be little doubt that *all* Mental processes are dependent, in the first instance, upon Sensations; which serve to the Mind the same kind of purpose that food and air fulfil in the economy of the body. If we could imagine a being to come into the world with its mental faculties fully prepared for action, but destitute of any power of receiving sensations, these faculties would never be aroused from the condition in which they are in profound sleep; and such a being must remain in a state of complete unconsciousness, because there is nothing which it can be made to feel, no kind of idea which can be aroused within it. But after the mind has once been in active operation, the destruction of all *future* power of receiving sensations would not reduce it again to this inactive condition; for sensations and ideas are so stored-up in the mind, by the power of Memory, that it can feed (as it were) upon the *past*.—Now the ideas which are excited by sensations, if associated with pleasurable or painful feelings, constitute those Emotions, or 'moving powers of the mind,' which are, either directly or indirectly, the springs of the greater part of our actions. When strongly excited, the emotions may produce movements which are purely 'automatic,' and which the Will may not be able to restrain; but in their normal exercise, they act in subordination to the Reasoning processes, and their operation upon the movements of the body is determined by the latter. The reasoning processes themselves may act not less 'automatically,' one idea suggesting another, and this again calling-forth another, in long succession, without any direction or control from the Will; and any idea thus excited with sufficient force, may express itself in bodily movement, if not prevented by the Will.—It is the peculiar character of a Volitional action, on the other hand, not only that it is the result of the exercise of the Reasoning powers, but that it is the expression of a definite *purpose*, of a *designed* adaptation of means to ends, on the part of the individual performing it; instead of proceeding from a mere blind indiscriminating impulse, such as that which is the mainspring of the instinctive and emotional actions, or being merely the result of a 'dominant idea,' which seems to be the case with the actions of many of the lower Animals.

633. Thus, then, we have to consider the Nervous system under three heads;—*first*, as the instrument of Reflex actions not involving sensation; —*second*, as the instrument of Consensual and Instinctive actions;—*third*, as the instrument of Mental processes, and of Voluntary movements. Now there is good reason to believe, that to each of these groups of actions a particular portion of the Nervous Centres, with its afferent and efferent nerves may be assigned; one ganglion, or series of ganglia, being

limited in its function to the reception of simple *impressions,* and to the origination of *reflex* movements consequent thereon; whilst another ganglion, or series of ganglia, is set-apart for the reception of impressions of which the mind becomes conscious as *sensations,* and for the origination of the *consensual* movements which these excite; whilst a third, which is superadded to the foregoing in Vertebrated animals, receiving from the proper sensorium the sensations which have been there called-up, is the instrument through which these sensations call *ideas* and *emotional feelings* into existence, by which these are employed in the various processes of *intellection,* and by which the *voluntary* determination is brought to bear upon the muscles. But we shall find reason to believe, that just as this Cerebral ganglion is called into action through the sensory portion of the apparatus to which it is added, so does it react through the motor portion of the same apparatus; and that it has no more direct connection with the muscular system, than it has with the organs of sense.

634. What has been hitherto said, refers exclusively to that division of the Nervous system, which is concerned in the reception of impressions, the production of sensations, and the stimulation of muscles to contraction; and as these are all purely animal functions, it has been called the *nervous system of animal life.* There is another set of ganglia and nerves, however, which constitutes what is termed the *Sympathetic* or visceral system; this is distributed to the various parts of the nutritive and secretory apparatus, its fibres forming a plexus upon the walls of the blood-vessels, and being distributed with them to all parts of the body; and hence it has been designated the *nervous system of organic life.* We have seen reason to believe, however, that the functions of Nutrition and Secretion are not themselves dependent upon nervous agency (§ 97); and the relation of the Sympathetic system to them, therefore, can scarcely be so intimate as that designation would seem to imply. Probably it is the vehicle for the involuntary action of the emotions upon those functions; and it may perhaps serve also to harmonise them with each other (§ 98). —We shall now take a brief survey of the comparative structure of the Nervous system in the principal groups of Animals, and enquire what actions may be justly attributed to its several parts in each instance; commencing with those in which the structure is the simplest, and the variety of actions the smallest; and passing-on gradually to those, in which the structure is increased in complexity by the addition of new and distinct parts, and in which the actions present a corresponding variety.

2. *Comparative View of the Structure and Actions of the Nervous System, in the principal groups of the Animal Kingdom.*

635. In the beings which have been associated under the designation of *Protozoa,* no definite traces of a Nervous System can be discovered; and it is maintained by many Physiologists, that, in these animals, the nervous matter is present in a "diffused form,"—that is to say, incorporated with the tissues; but it would be difficult to assign a valid reason for a supposition so gratuitous. An arrangement of this kind cannot be required to confer on the individual parts of the organism their vital properties; since these exist, to as great an extent, in beings which are allowed to be entirely destitute of it, namely the entire Vegetable kingdom. The simplest office of a nervous system is, as we have seen (§ 630),

to establish a communication between parts specially modified to receive impressions, and others particularly adapted to respond to them. Where every portion of the body has similar endowments, there can be no object in such a communication; just as, where every part of the surface is equally capable of Absorption, and every part of the tissue equally permeated by nutrient fluid, there is no necessity for a Circulating system. A nervous system would seem to be required only in a being possessed of a number of distinct organs, whose actions are of such a character that they cannot be brought into mutual relation, without a more immediate and direct communication than that afforded by the circulating system, which, as we have seen, is the only bond of union possessed by Plants between distant parts. In the lowest and simplest Animals, whatever degree of contractility exists, appears to be almost equally diffused through the system; and we neither find any special sensory organs, adapting one part more than another to the reception of impressions, nor do we observe any portion of the structure peculiarly endowed with the power of motion; neither can we discover anything like a nervous system fitted to receive such impressions, and to excite respondence to them in distant parts. To use the forcible expression of Sir Gilbert Blane—" Mr. Hunter, by a happy turn of expression, calls the function of the nervous system *internuncial.* It is evident that some such principle must exist in the complicated system of the superior Animals, in order to establish that connection which constitutes each individual a WHOLE." But where all the parts act *by* and *for* themselves, there is no necessity for such an internuncial communication; and consequently, although, when united, their functions all tend towards the maintenance of the system to which they belong, they are capable of being separated from it and from each other, without these functions being necessarily abolished. The motions exhibited by Animals of these lowest classes, would seem to be scarcely less directly dependent upon external stimuli, than are those of Plants; being, in fact, the result of the general diffusion of that exalted degree of irritability, which is restricted in most plants to particular parts of the structure (§ 624). Of the degree of sensibility which they may enjoy, we have no adequate means of forming a judgment; but if they do possess *any* consciousness of external impressions, it is probably diffused through the whole structure alike. And thus the endowments which we find to be restricted among the higher Animals, by the differentiation of their organization, to special kinds of tissue, and which are only fully manifested by the instrumentality of these, may be conceived to belong in a more generalized form to the entire fabrics of the lower.—(See GENERAL PHYSIOLOGY.)

636. No valid ground can be shown for assigning any higher character to the movements of *Zoophytes,* such as the *Hydra* or *Actinia,* and their composite allies; since all those actions which are concerned in the prehension and ingestion of food, are, as already remarked, really analogous rather to the peristaltic movements of the œsophageal muscles and stomach of higher animals, than to the motions of their limbs; and the few which they exhibit, that are not referable to this category, appear to be the result of the direct stimulation of light or other physical agencies, which may operate by producing organic changes in their tissues, as in those of Plants. At any rate it may safely be affirmed, that if these

Zoophytes do possess any rudiment of a Nervous System, and if any of their actions are to be attributed to its instrumentality, its participation in the general course of their vital actions must be very trifling. We have at present, it must be acknowledged, no certain means of appreciating the degree of sensibility possessed by these lowest members of the Animal kingdom. The motions which follow the impressions of external agents, are our only means of judging of its possession by a particular being; and in the interpretation of these phenomena, the greatest care is requisite to avoid being misled by false analogies. Much error has probably arisen, from comparing the manifestations of life exhibited by creatures of this doubtful character, with those of the highest Animals; and thence inferring that, because motions are witnessed in the former which bear some analogy to those of the latter, they must be equally dependent on a nervous system. But, when it is considered how completely vegetative is the life of such beings, and how closely all their motions are connected with the performance of their organic functions, it would seem obvious that the general comparison should be made with Plants, rather than with Animals; and that we should seek the assistance of principles of a higher character, only when those we already possess are insufficient to explain the phenomena.

637. It is in the higher *Radiata*, that we find the first definite indications of the existence of a connected Nervous system. It is probable that such exists in all the *Acalephæ*, although the softness of their tissues renders it difficult of detection. According to Ehrenberg, two nervous circles may be detected in the *Medusa;* one running along the margin of the mantle and furnished with eight ganglia, from which filaments proceed to the eight red spots which he supposes to be eyes; whilst the other is disposed around the entrance to the stomach, and is furnished with four ganglia, from which filaments proceed to the tentacula. A nervous ring has also been detected by Prof. Agassiz in *Sarsia*, one of the 'naked-eyed' Pulmogrades; and he states that it is entirely composed of ganglionic cells.*. In *Beroe*, it is affirmed by Dr. Grant that a nervous ring exists round the mouth, furnished with eight ganglia, from each of which a filament passes towards the other extremity of the body, while others are sent to the lips and tentacula.—In the *Echinodermata*, however, its manifestations are much less equivocal. In the *Asterias*, for instance, a ring of nervous matter surrounds the mouth, and sends three filaments to each of the rays; of these, one seems to traverse its length, while the two others are distributed on the cæcal prolongations of the stomach. In the species examined and figured by Tiedemann, no ganglionic enlargements of this ring appear to exist, and it seems not improbable that, as in the Medusæ, the entire ring is composed of vesicular nervous matter; but this element is usually collected into distinct ganglia, which are found at those points of the ring whence the branches diverge, the number of the ganglia being always equal to that of the rays. In those species which possess ocelli at the extremities of the rays, the nervous

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* "Contributions to the Natural History of the Acalephæ of North America," Part I., p. 232.—It is considered by Prof. Agassiz that the movements of these Acalephæ are 'voluntary' and exhibit 'a purpose;' but his statements on this subject exhibit a very strange confusion of ideas; and the Author is assured by Mr. Huxley that he has never seen the slightest evidence of anything beyond 'automatic' action in these animals.

cord proceeding towards each, swells into a minute ganglion in its neighbourhood.—In the *Echinus*, the arrangement of the nervous system follows the same general plan; the filaments which diverge from the oral ring being distributed (in the absence of rays) to the complicated dental apparatus, whilst others pass along the course of the vessels to the digestive organs. The transition between the Radiata and Articulata, presented by the *Holothuria* and *Sipunculus*, is peculiarly well marked in the nervous system of these animals; for the ring which encircles the mouth is here comparatively small, but a single or double non-gangliated filament traverses the length of their prolonged bodies, running near the abdominal surface (which is their situation in the Articulated classes) and giving-off transverse branches.

638. When we compare the character of the nervous system of these *Radiated* classes, with that of higher Animals of more heterogeneous structure, we find that every segment of the body which is similar to the rest, is connected with a ganglionic centre, that seems to be subservient to the functions of its own division alone, and to have little communication with, or dependence upon, the remainder; these centres being all apparently similar to each other in their endowments. This is the case, indeed, not merely with the tribes we are now considering, but with the lower Articulata; the chief difference being, that the individual portions are here disposed in a radiate manner round a common centre, whilst in the latter they are longitudinally arranged. But when the different organs are so far specialized as to be confined to distinct portions of the system, and each part consequently becomes possessed of a different structure, and is appropriated to a separate function, this repetition of parts in the nervous system no longer exists; its individual portions assume special and distinct offices; and they are brought into much closer relation to one another, by means of the *commissures* or connecting fibres, which form a large part of the nervous masses in the higher Animals. It is evident that, between the most simple and the most complex forms of this system, there must be a number of intermediate gradations,—each of them having a relation with the general form of the body, its structure and economy, and the specialization of its distinct functions. This will be found, on careful examination, to be strictly the case; and yet, with a diversity of its parts, as great as exists in the conformation of any other organs, its essential character will be found to be the same throughout.

639. Among the *Molluscous* classes, there is no radiate or longitudinal multiplication of parts, the only repetition being on the two sides of the median plane. It is chiefly in the organs of animal life, that this bi-lateral symmetry is observable, the symmetry of their nutritive apparatus being obscured by the unequal development of its different parts (§ 41); and the predominance of the latter in their organization impresses itself (so to speak) upon their Nervous System, which is not formed until a late period of development (§ 565), and which shows a want of constancy in the relative position of its centres, that is in striking contrast with the uniformity of plan which is so obvious in the nervous systems of Articulata and Vertebrata. Of these centres, there are typically three pairs:—1. The *Cephalic* ganglia, which lie either at the sides of the œsophagus, or above it, and may be either disjoined, although

connected by a commissure, or fused into one mass which is usually bilobed; this gives-off nerves to the labial and olfactory tentacula, to the eyes, and to the muscular apparatus of the mouth; and upon either of these nerves, accessory ganglia may be developed.—2. The *Pedal* ganglia, which are commonly fused into one mass which is situated below the œsophagus, and are connected with the cephalic ganglia by a commissural band on each side, forming a ring which encircles that canal; though, in the *Nudibranchiata* and some other Gasteropods, the pedal ganglion of each side is fused into one mass with the corresponding cephalic ganglion: from the pedal ganglion are given-off nerves to the foot, and also to the organs of hearing when these are not actually lodged in them, as frequently happens.—3. The *Parieto-splanchnic* ganglia, which are usually found in the posterior part of the body, and are connected by commissural bands both with the cephalic and with the pedal ganglia; these give-off nerves to the muscular and sensitive parietes of the body, to the shell-muscle or muscles, to the branchial apparatus, and to the heart and large vessels. The function of these is divided, in the higher Mollusca, between two or more pairs of ganglia; and the proper visceral or sympathetic system becomes more distinct from it.*

640. No such differentiation of function presents itself, however, among the lowest Mollusca, namely, the *Bryozoa* and *Tunicata*. In many of the former group, but most distinctly in the fresh-water species, a small body may be seen at the base of the tentacular circle (Fig. 49, A, *a*), between the oral and anal orifices; which, from its appearance, and its correspondence in position with the undoubted ganglion of the Tunicata, may be regarded almost with certainty as a nervous centre. No branches, however, have been seen to proceed from it, either to the tentacula, or to the muscles; but the activity of the movements of these animals, with the perfection of their muscular structure (the fibres being striated in many species), would seem to indicate that nervous instrumentality is concerned in them.—In the Tunicata there is no difficulty in discovering the nervous ganglion, which is always situated between the oral and anal orifices (Fig. 121, *j*), being sometimes single, and sometimes bilobed or even double; this ganglion is connected by branches with the sensory tentacula which guard the oral orifice, and branches extend from it also over the muscular coat of the branchial sac, filaments being specially transmitted to the oral and anal sphincters.—No beings possessed of a complex internal structure, a distinct stomach and alimentary tube, a pulsating heart and ramifying vascular apparatus, with branchial appendages for aerating the blood, and highly-developed secretory and reproductive organs, can be imagined to spend the period of their existence in a mode more completely vegetative than these. The continuous and equable current of water which enters the cavity of the mantle, and which serves at the same time to convey food to the stomach and to aerate the blood, is maintained, without any nervous agency, by the vibrations of the cilia with which the walls of the cavity are clothed; and it is only when substances come in contact with the sensitive tentacula, which ought not to enter the orifice, or when they have been introduced and are to be expelled, or when some external irritation is applied, that we

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* See Huxley 'On the Morphology of the Cephalous Mollusca,' in "Philos. Transact.," 1853, pp. 52, *et seq.*

see anything like a definite muscular movement, indicating the agency of a nervous system. The ganglion appears to control the circular sphincters which surround the orifices of the mantle, as well as the muscular fibres which are spread in a network over the whole sac; by the contraction of the former, the ingress of improper substances is prevented; and by that of the latter, the fluid contained in the cavity is violently ejected, as occurs when the animal is subjected to any external contact, or is excited to the same action by any internal irritation. This ganglion, then, must be regarded as chiefly *parieto-splanchnic;* and from the analogy of higher animals, we should be led to regard its actions as altogether 'automatic,' the movements just described being analogous to those of coughing and sneezing in Man. Rudimentary organs of vision and of hearing, however, are found in some Tunicata, so that we must regard this ganglion as the seat of whatever consciousness these animals may possess; and from the distribution of the nerves which are connected with it, this single centre must be considered as combining in itself the functions which are elsewhere distributed among several.

641. The type of the Nervous system in the group of *Brachiopoda* presents but little advance upon the foregoing; the chief difference being, that the greater disconnection of the two lateral halves of the body keeps those ganglionic centres distinct, which are fused into a single mass among the mollusks of the preceding group. These centres are sub-œsophageal in their position; but they are connected together, not merely by a commissural band beneath the œsophagus, but by another which arches-over it; so that a complete ring is formed, through which the œsophagus passes. From the distribution of the nerves to the spiral arms, to the mantle, and to the viscera, it is evident that these ganglionic centres are to be regarded as uniting the functions of *pedal* and *parieto-splanchnic* ganglia; whilst the existence of a supra-œsophageal commissure indicates that they represent also the cephalic ganglia, although no rudiments of special-sense organs or nerves have been yet detected in this group.*

642. The separation of the Nervous centres, and the differentiation of their function, is carried to a greater extent in the *Lamellibranchiate* bivalves, in accordance with the higher development of the general organisation; but the parieto-splanchnic ganglion is still the principal one, and this is found near the posterior extremity of the body. At the sides of the œsophagus, there are seen two small *labial* or *cephalic* ganglia (Fig. 271, *a*, *a*), united by a band which arches over it, and usually, also, by another pair of filaments which meet beneath it; in some of the higher Conchifera (such as the *Mactra*), however, these two ganglia nearly coalesce into a single mass above the œsophagus. These ganglia are connected by nervous filaments (probably of an *afferent* character) with the sensory tentacula that guard the oral orifice; they send a pair of branches (the 'anterior palleal'), which in the *Solen* are of considerable size, to the anterior portion of the mantle and to the anterior adductor muscle; a pair of trunks (*e*) which enter the *parieto-splanchnic* ganglion, whose branches are extensively distributed to all parts of the respiratory

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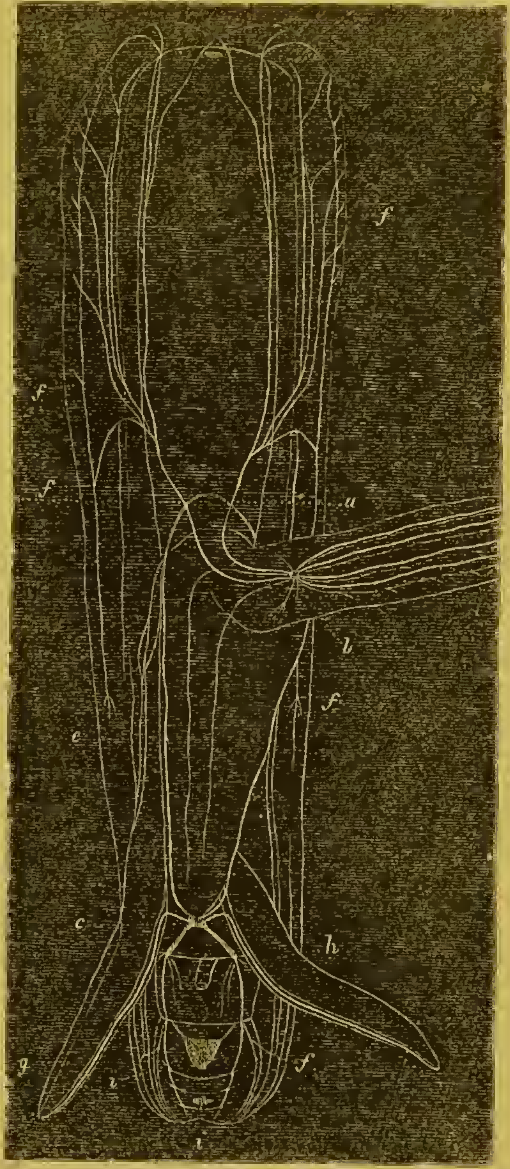
* See Prof. Owen on the 'Anatomy of the Terebratula,' in the Introduction to Mr. Davidson's Monograph on the "British Fossil Brachiopoda," p. 11.

apparatus, siphons, &c., and also to the posterior part of the mantle ('posterior palleal' branches) and to the adductor muscle. The anterior and posterior palleal nerves of either side usually inosculate to form a 'circumpalleal' nerve, which passes round the margin of each lobe of the mantle, and supplies branches not only to its muscular substance, but also to the sensory organs (such as the tentacula of *Lima*, and the eyes of *Pecten*,) with which it is often furnished; these trunks are frequently studded, as in *Solen*, with minute ganglia (*f*, *f*) in different parts of their course; and where none such are met-with, it is stated by Duvernoy that the nerves themselves contain ganglionic cells, so as in fact to constitute elongated ganglia. In those *Lamellibranchiata* which possess a foot, a third principal nervous centre, the *pedal* ganglion (*b*), is found at its base, and seems peculiarly connected with its actions; but where the foot is absent, as in the *Oyster* tribe, this either does not exist, or is only represented by a pair of minute ganglia situated immediately behind the cephalic. The pedal ganglion has always an immediate connection with the cephalic; and in general, this connection is quite distinct from that of the parieto-splanchnic, so that the pedal and parieto-splanchnic ganglia have not even an apparent connection with each other. Sometimes, however, the pedal ganglion has no such obviously-distinct communication with the cephalic, being situated on the nervous cords which pass backwards from the cephalic to the parieto-splanchnic; and the pedal and parieto-splanchnic ganglia thus seem to be connected together. The normal relations of the parts, however, are not altered by such an arrangement; for the trunks which connect the parieto-splanchnic ganglia with the cephalic pass *over*, not *through*, the pedal, which has its own bands of union as structurally distinct

Fig. 271.



Nervous system of *Solen*;—*a*, *a*, cephalic ganglia, connected by a transverse band arching over the œsophagus; *b*, pedal ganglion, the branches of which are distributed to the powerful muscular foot; *c*, parieto-splanchnic ganglion, the branches of which proceed to the gills *g*, the siphons, *i*, *i*, and other parts; *e*, trunks connecting the cephalic and parieto-splanchnic ganglia; *f*, *f*, *f*, *f*, minute ganglia on the palleal branches; *h*, anus.

as in the Solen.—No satisfactory evidence has yet been adduced, of the separate existence of a Sympathetic or *visceral* system of nerves in this group.*

643. A good deal of variety exists in this class, in regard to the actions to which the nervous system is subservient. Many of those which have no foot (such as the *Oyster*) are attached for life to the place where they originally fix themselves; and no evident motion is exhibited by these, save the opening and closure of the shell, which corresponds with the dilatation and contraction of the sac of the mantle in the Tunicata. This is principally accomplished by the posterior ganglion, which supplies the adductor muscle. Other species, being unattached, are enabled to swim by the flapping of the valves in the water. Among those which have a foot, this organ is employed for many different purposes, such as burrowing, leaping, &c.; which are generally executed in such a manner, as to imply that they are in some degree under the direction of consciousness. And it is in the most free and active of these Bivalves, that we have the most distinct indications of the presence of organs of special sensation; these, however, where they exist, are not restricted to any particular part of the body, but are disposed along the free margins of the lobes of the mantle. For reasons which will be given hereafter, it appears probable that, whilst the *general* movements of the foot are directed by the cephalic ganglia, under the guidance of sensations, the *particular* actions by which it fixes itself on a given surface, and adapts its disk to the inequalities which it encounters, may be produced simply by impressions conveyed to its own ganglion through its afferent nerves, and reflected through its motor fibres, in which sensations are not necessarily concerned. The same may be inferred respecting the actions of the parieto-splanchnic ganglion; which, so far as they participate in the respiratory function, may probably be considered as simply-reflex; but when the adductor muscle is caused by it to draw-together the valves, either for protection from threatened injury, or for the propulsion of the body through the water, the movement being prompted or directed by consciousness, we must regard the cephalic ganglia as its original source.—The whole course of the lives of these animals shows them to be so little elevated in the scale of psychical endowment, that we can scarcely regard any of the motions executed by them as possessing a truly voluntary character. The greater part of them are concerned in protecting the animal from danger, and in the prehension of its food; and may be compared in the higher animals to the closing of the glottis against irritating matters, and to the contraction of the pharynx in swallowing.

644. As the Head is not otherwise indicated, in the two preceding classes of Mollusca, than by the position of the mouth, and as the organs of special sensation are but very imperfectly evolved, it is not to be wondered-at that the cephalic ganglia should be inferior in size to those more connected with powerful and active muscles. But in the higher classes it is very different; and in proportion as we meet with evidence of the possession of the senses of sight, hearing, &c., and find these organs no longer scattered over the periphery of the body, but collected

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* For the Anatomy of the Nervous system of *Lamellibranchiata*, see especially Garner in "Linnæan Transactions," Vol. XVII.; Blanchard in "Ann. des Sci. Nat.," 3e Sér., Zool., Tom. III.; and Duvernoy, Op. cit., Tom. XVIII.

upon a 'head,' do we observe a greater concentration of the ganglionic system towards their neighbourhood.—In the *Pteropoda* and *Heteropoda*, the general distribution of the nervous system is not very dissimilar to that which has been last described. Thus, in *Carinaria*, the cephalic ganglia are still found separate, lying at the sides of the œsophagus, and connected by a transverse band; and these receive the optic nerves and tentacular filaments. Besides other branches transmitted to the neighbouring organs, two principal trunks are sent backwards, which unite in a large ganglion situated among the viscera; and from this nerves proceed to the foot, respiratory organs, and posterior part of the trunk; so that it may be regarded as combining the functions of the pedal and parieto-splanchnic ganglia, as is further indicated by its quadrilobate form. In *Gasteropoda*, however, the cephalic ganglia are generally much larger in proportion to the rest, than they are in Acephala; and they show a tendency to approximate each other, and to gain a position *above* the œsophagus, as we see in *Paludina* (Fig. 44, *u*, *u*); or even to meet upon it in a single mass, as in *Aplysia* (Fig. 50, *d*). The parieto-splanchnic ganglia are not unfrequently represented by two distinct pairs of centres, which may be termed, from the distribution of their respective nerves, the 'branchial,' and the 'palleal.' The *branchial* ganglion is generally found in the immediate neighbourhood of the respiratory organs, and its position, therefore, is as variable as theirs (§ 291): it is not unfrequently conjoined into one mass with the pedal or palleal centres; but its presence may always be recognised by the distribution of its nerves, as well as by its separate connection with the cephalic ganglia. The position of the *pedal* ganglion, which is constantly found in the Gasteropoda, and which is generally *double* though the foot is single, also varies, but in a less degree; since it is usually near the ventral surface, at no great distance behind the head. The *palleal* ganglia are sometimes united with the branchial, sometimes with the pedal, according, perhaps, as the movements of the mantle most participate in the respiratory acts, or in the general locomotion of the body; but they are recognised by the distribution of their nerves, and by their separate connection with the cephalic ganglia. Thus in Aplysia, the cord of communication which unites the single supra-œsophageal ganglion (Fig. 50, *d*) with the two infra-œsophageal ganglia (*e*, *e*), is triple; the latter are known, by the distribution of their nerves, to combine the functions of pedal and palleal ganglia, whence we can account for their double connection with the cephalic; and the third cord passes *through* them to the branchial ganglion (*m*), which is single, and lies at the posterior part of the body. The pedal, branchial, and palleal ganglia are all found separate from one another in some instances; while in other cases they are all brought together in the neighbourhood of the œsophagus. This last is the usual arrangement in the 'naked' Gasteropods, whether pulmonated or branchiferous. It is in the *Pulmonata* that the concentration is carried to its greatest extent; thus in the *Slug*, we find but a single nervous mass beneath the œsophagus, in which the three pairs of ganglia have become fused. In the *Nudibranchiata*, on the other hand, these ganglionic centres for the most part remain distinct, although they are aggregated-together; and in these, moreover, the number of nervous centres is further multiplied by the development of distinct ganglia in connection with the olfactory and optic nerves.—Besides the foregoing ganglia and nerves, we find, in many of the Gasteropoda, a separate system connected with the complicated apparatus of manducation and deglutition, which this class usually possesses. The nerves which supply these organs do not proceed from the cephalic ganglia, but from a distinct centre, which is usually placed in advance of them upon the mouth or pharynx; and their ramifications proceed also along the œsophagus to the stomach. This set of nerves and ganglia, which is even more important from its relative development in other classes, may be called from its distribution the *stomato-gastric* system. We shall see that analogous ganglionic centres, and nerves of very similar distribution, exist in Vertebrata; but that they no longer constitute a distinct apparatus, being fused, as it were, into the general Cerebro-spinal system.—A distinct *visceral* or Sympathetic system of nerves; consisting of a multitude of minute ganglia and of a network of filaments, dispersed through the various parts of the apparatus of organic life, and communicating with the stomato-gastric system, has now been clearly made-out among the Nudibranchiate Gasteropods, and probably exists elsewhere.*

645. In our examination of the Nervous System of the Mollusca, we hitherto met with a progressive multiplication of its centres, in accordance with the progressive complication of the organism, and especially with the increase of its sensori-motor powers. To those simply 'reflex' actions immediately connected with the maintenance of organic life, we have found that general locomotive movements are superadded, which, as they involve the guidance of sensations, must be regarded as belonging to the 'consensual' class; and as a distinct foot is developed, the muscular coat of the mantle thickened, a complicated apparatus for the reduction of the food provided, and more perfect organs of special sense evolved, do we find a corresponding development of ganglia which are their centres of action. In no instance, however, are these ganglia repetitions of each other, except on the two sides of the median line; and there is no evidence that the cephalic ganglia have any other function, than that of receiving sensory impressions, communicating them (so to speak) to the consciousness, and calling forth respondent muscular movements. Nor is there anything in the habits of life of these animals, which indicates that their actions are of a nature above the automatic.

646. The Nervous System of the *Cephalopoda* exhibits an obvious approach towards that of Vertebrated animals, in the concentration of the cephalic ganglia into one mass, which, though still perforated by the œsophagus, lies almost entirely above it, and is sometimes protected by plates of cartilage that constitute the rudiment of a neuro-skeleton. In the *Nautilus*, however, which is the type of the inferior or *Tetrabranchiate* order of this class, the general distribution of this system corresponds pretty closely with that seen in the higher Gasteropoda. The œsophagus is still encircled with a ganglionic ring, of which the upper part gives off the optic nerves, whilst the lower supplies the mouth and tentacula, and sends trunks backwards into the shell. The trunk

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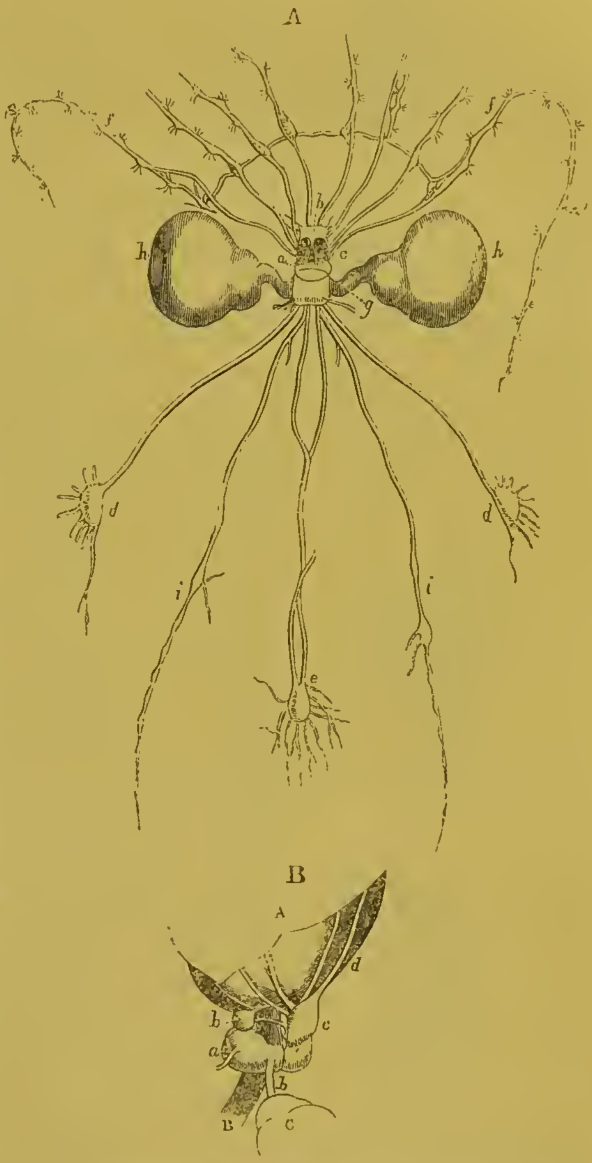
* See the admirable Memoir 'On the Anatomy of Doris,' by Mr. Hancock and Dr. Embleton, in "Philos. Transact.," 1852, and the 'Anatomy of Eolis' in Alder and Hancock's "Monograph on the Nudibranchiate Mollusca," published by the Ray Society. See also Mr. Garner's Memoir already referred-to, and M. Blanchard's 'Recherches sur l'Organisation des Opisthobranches,' in "Ann. des Sci. Nat.," 3e Sér., Zool., Tom. IX.

which supplies the internal tentacula, and what is probably the olfactory organ, has a small ganglion situated upon it; and other ganglia, which probably belong to the stomato-gastric and sympathetic systems, are found on the nerves distributed to the viscera. In the *Dibranchiate* order, whose habits are more active, and whose general organisation is higher, we find a somewhat different arrangement (Figs. 272-274). The organ of vision here attains an increased development and importance; an organ of hearing evidently exists; and the whole surface of the body is possessed of sensibility. In *Argonauta*, the *cephalic* ganglia are united into a single large mass on the median line (Fig. 272, *a*), from the lateral portions of which the optic nerves are given-off; but in *Sepia* and *Octopus*, the optic ganglia (Figs. 273, 274, *b*, *b*) are distinct from the median portion, which is considered by Prof. Owen as an olfactive ganglion. The nerves which supply the buccal apparatus are usually connected with a distinct ganglion in advance of the cephalic (Fig. 272, *b*, Fig. 274, *e*); but sometimes this ganglion is fused into the general mass, as happens in Octopus (Fig. 273). Besides this *buccal* ganglion, we find in Sepia a *labial* ganglion (Fig. 274, *f*), which supplies the parts immediately surrounding the entrance to the mouth. The nerves which supply the arms, proceed, in all Cephalopods, from the anterior part of the sub-œsophageal mass, which constitutes the *pedal* ganglion; and in the Dibranchiata, whose arms are furnished with suckers, the nerve-trunks (Fig. 272, *f*, *f*) are beset with a series of accessory ganglia in connection with those organs, every sucker possessing a ganglion of its own. It has been shown by Dr. Sharpey, that the principal

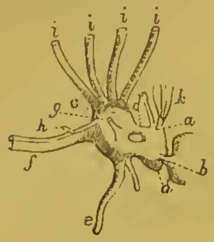
Fig. 272.



Nervous system of *Argonauta argo*; A, as seen in front; B, as viewed in profile, showing the relations of the nervous centres to the buccal mass A, the œsophagus B, and the eye C;—*a*, cephalic ganglion; *b*, buccal ganglion; *c*, sub-œsophageal ganglion; *d*, *d*, stellate ganglia of the mantle; *e*, visceral ganglion; *f*, nerves of the arms, with ganglionic enlargements; *g*, optic nerves; *h*, *h*, eyes; *i*, *i*, branchial nerves with their ganglia.

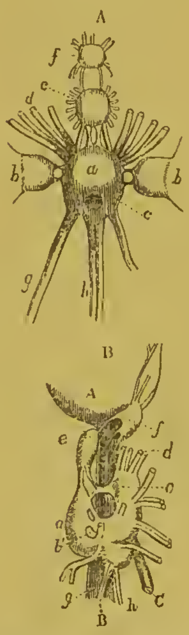
trunk of each arm may be divided into two distinct tracts; in one of which there is nothing but *fibrous* structure, forming a direct communication between the suckers and the central ganglia; whilst in the other are contained the *ganglia* which peculiarly appertain to the suckers, and which are connected with them by distinct filaments: so that each sucker has a separate relation with a ganglion of its own, whilst all are alike connected with the cephalic ganglia, and are placed under their control. We see the results of this arrangement, in the modes in which the contractile power of the suckers may be called into operation. When the animal embraces any substance with its arm (being directed to this action by its sight or other sensation), it can bring all the suckers simultaneously to bear upon it; evidently by the transmission of an impulse along the motor cords, that proceed from the central ganglia to the suckers. On the other hand, any individual sucker may be made to contract and attach itself, by placing a substance in contact with it alone; and this action will take place equally well, when the arm is separated from the body, or even in a small piece of the arm when recently severed from the rest,—thus proving that, when it is directly excited by an impression made upon itself, it is a *reflex* act, quite independent of the cephalic ganglia, not involving sensation, and taking place through the medium of its own ganglia alone. In the *Octopus*, which swims by a kind of circular fin that is formed by a membrane connecting the tentacula, a curious connection exists between the nerves radiating to these from the cephalic ganglia; for, at the base of the arms, a nervous ring is found (like that of the Asterias § 637), which unites them all, and probably contributes to harmonise their actions.—From the posterior part of the sub-œsophageal mass, proceed the nerve-trunks which supply the general surface of the mantle; and these enter two large stellate ganglia (Fig. 272, *d, d*), before separating into their ramifications. Other trunks, also furnished with ganglia of their own (*i, i*), supply the respiratory apparatus; and in the centre we find a single or double trunk, which passes towards the digestive apparatus, and enters the visceral ganglion (*e*). There can scarcely be a doubt of the existence of a separate Sympathetic system; although it has not yet been made-out.—Thus we have traced in the Cephalopoda, the highest development of a nervous system formed to minister chiefly to the sensorial and nutritive functions; we shall now follow that of the Articulata, in which the locomotive powers are especially predominant;

Fig. 273.



Nervous centres of *Octopus;*—*a*, pharyngeal ganglion; *a'*, proper cephalic ganglion; *b*, optic ganglion; *c*, sub-œsophageal ganglion; *d*, aperture giving passage to the œsophagus; *e*, one of the great palleal nerves; *f*, principal visceral nerve; *g*, nerve of the funnel; *h*, auditory nerves; *i, i, i, i*, nerves of the arms; *k*, buccal nerves.

Fig. 274.

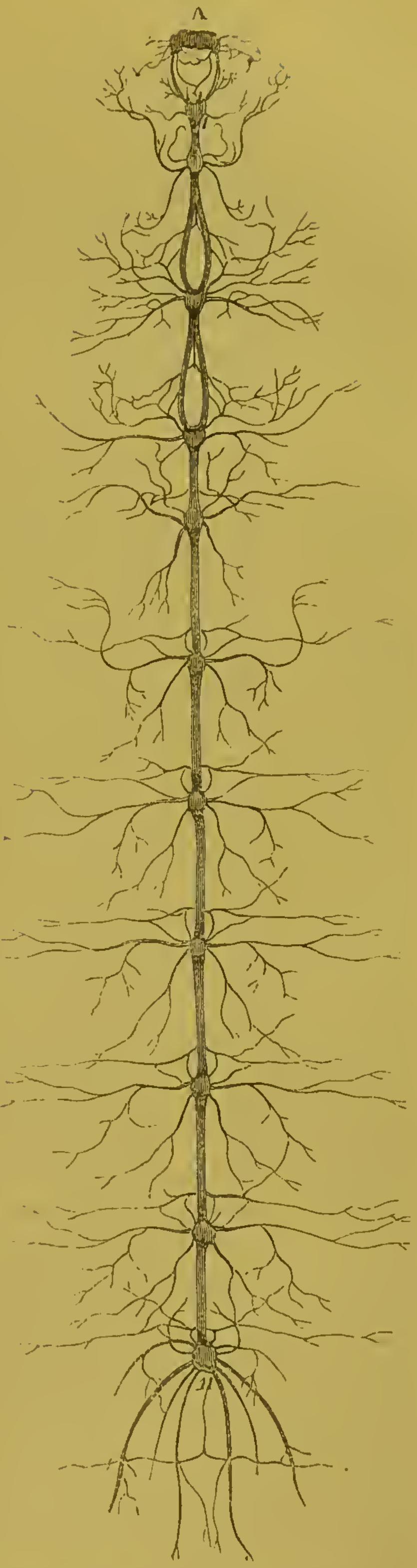


Nervous centres of *Sepia officinalis;*—A, viewed from above; B, the same as seen from the side, with its relations to A, the buccal mass, B, the œsophagus, and C the aorta;—*a*, cephalic ganglion; *b, b*, optic ganglia; *c*, sub-œsophageal ganglion; *d, d*, nerves of the arms; *e*, buccal ganglion; *f*, labial ganglion; *g*, nerves of the mantle; *h*, visceral nerve.

and we shall afterwards find that the Vertebrata combine the types characteristic of both.

647. The plan on which the Nervous system is distributed in the sub-kingdom *Articulata*, exhibits a remarkable uniformity throughout the whole series; whilst its character gradually becomes more elevated, as we trace it from the lowest to the highest divisions of the group. It usually consists of a double nervous cord, studded with ganglia at intervals; and the more alike the different segments, the more equal are these ganglia. The two filaments of the nervous cord are sometimes at a considerable distance one from the other, and their ganglia distinct; but more frequently they are in close apposition, and the ganglia appear single and common to both. That which may be regarded as the typical conformation of the nervous system of this group, is seen in the ganglionic cord of *Scolopendra*, or in that of the larva of most Insects, such as that of *Sphinx ligustri* (Fig. 275). Here we see the nervous cord nearly uniform throughout, its two halves being separated, however, at the anterior portion of the body; the ganglia are disposed at tolerably-regular intervals, are similar to each other in size (with the exception of the last, which is formed by the coalescence of two), and every one supplies its own segment, having little connection with any other. The two filaments of the cord diverge behind the head, to enclose the œsophagus; above which we find a pair of ganglia, that receive the nerves of the eyes and antennæ. We shall find that, in the higher classes, the inequality in the formation and office of the different segments, and the increased powers of special sensation, involve a considerable change in the nervous system, which is concentrated about the head and thorax. In the simplest Vermi-

FIG. 275.



Nervous system of Larva of *Sphinx ligustri*; A, cephalic ganglia; 1-11, ganglia of the trunk.

form tribes, on the other hand, we lose all trace of separate ganglia, the nervous cord passing without evident enlargement from one extremity to the other. Whatever may be the degree of multiplication of the ganglia of the trunk, they seem but repetitions one of another; the functions of each segment being the same with those of the rest. The *cephalic* ganglia, however, are always larger and more important; they are connected with the organs of special sense; and they evidently possess a power of directing and controlling the movements of the entire body, whilst the power of each ganglion of the trunk is confined to its own segment.—The longitudinal gangliated cord of Articulata occupies a position which seems at first sight altogether different from that of the nervous system of Vertebrated animals; being found in the neighbourhood of the *ventral* or inferior surface of their bodies, instead of lying just beneath their *dorsal* or upper surface. From the history of their development (§ 582), however, and from some other considerations, it has been suggested that the *whole* body of these animals may be considered as in an inverted position; the part in which the segmentation is first distinguished in Insects being the real equivalent of the dorsal region in Vertebrata, and that over which the germinal membrane is the last to close-in, being homologous with the ventral region. This view applies also to the position of the 'dorsal vessel,' which would then be on the ventral side of the axis, as in Vertebrata. Regarded under this aspect, the longitudinal nervous tract of Articulata corresponds with the Spinal cord of Vertebrated animals in *position*, as we shall find that it does in *function.*

648. When the structure of the chain of ganglia is more particularly inquired-into, it is found to consist of two distinct tracts; one of which is composed of nerve-*fibres* only, and passes backwards from the cephalic ganglia, over the surface of all the ganglia of the trunk, giving-off branches to the nerves that proceed from them; whilst the other includes the *ganglia* themselves (Fig. 277, A). Hence, as in the Mollusca, every part of the body has two sets of nervous connections; one with the cephalic ganglia; and the other with the ganglion of its own segment. Impressions made upon the afferent fibres, which proceed from any part of the body to the cephalic ganglia, become *sensations* when conveyed to the latter; whilst, in respondence to these, the *consensual* impulses, operating through the cephalic ganglia, harmonize and direct the general movements of the body, by means of the efferent nerves proceeding from them. For the lower reflex operations, on the other hand, the ganglia of the ventral cord are sufficient; each one ministering to the actions of its own segment, and, to a certain extent also, to those of other segments. It has been ascertained by the careful dissections of Mr. Newport, to whom we owe all our most accurate knowledge of the structure of the Nervous system in Articulated animals,* that of the fibres constituting the roots by which the nerves are implanted in the ganglia, some pass into the vesicular matter of the ganglion, and, after coming into relation with its vesicular substance, pass-out again on the same side (Fig. 276, *f*, *k*); whilst a second set, after traversing the vesicular matter, pass-out by the trunks proceeding from the opposite side of the same ganglion; whilst a

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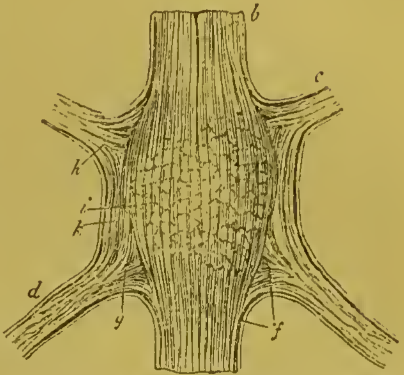
* See his successive papers in the "Philosophical Transactions" from 1832 to 1843, and particularly his Memoir on the 'Nervous System of Myriapoda' in the last-named year.

third set run along the portion of the cord which connects the ganglia of different segments, and enter the nervous trunks that issue from them, at a distance of one or more ganglia above or below. Thus it appears, that an impression conveyed by an afferent fibre to any ganglion, may excite motion either in the muscles of the same side of its own segment; or in those of the opposite side; or in those of segments at a greater or less distance, according to the point at which the efferent fibres leave the cord. And as the function of these ganglia is altogether related to the locomotive actions of the segments, we may regard them as so many repetitions of the *pedal* ganglia of the Mollusca; their multiplication being in precise accordance with that of the instruments which they supply.

FIG. 276.



Portion of the ganglionic tract of *Polydesmus maculatus*:—*b*, inter-ganglionic cord; *c*, anterior nerves; *d*, posterior nerves; *f*, *k*, fibres of reflex action; *g*, *h*, commissural fibres; *i*, longitudinal fibres, softened and enlarged, as they pass through ganglionic matter.

649. The general conformation of Articulated animals, and the arrangement of the parts of their Nervous system, render them peculiarly favourable subjects for the study of the simplest *reflex* actions; some of the principal phenomena of which will now be described.—The *Mantis religiosa* customarily places itself in a curious position, especially when threatened or attacked, resting upon its two posterior pairs of legs, and elevating its thorax with the anterior pair, which are armed with powerful claws: now if the anterior segment of the thorax, with its attached members, be removed, the posterior part of the body will still remain balanced upon the four legs which belong to it, resisting any attempts to overthrow it, recovering its position when disturbed, and performing the same agitated movements of the wings and elytra as when the unmutilated insect is irritated; on the other hand, the detached portion of the thorax, which contains a ganglion, will, when separated from the head, set in motion its long arms, and impress their hooks on the fingers which hold it.—If the head of a *Centipede* be cut-off, whilst it is in motion, the body will continue to move-onwards by the action of the legs; and the same will take place in the separate parts, if the body be divided into several distinct portions. After these actions have come to an end, they may be excited again, by irritating any part of the nervous centres, or the cut extremity of the nervous cord. The body is moved forwards by the regular and successive action of the legs, as in the natural state; but its movements are always forwards, never backwards, and are only directed to one side, when the forward movement is checked by an interposed obstacle. Hence although they might *seem* to indicate consciousness and a guiding will, they do not so in reality; for they are carried-on, as it were, mechanically; and show no direction of object, no avoidance of danger. If the body be opposed in its progress by an obstacle of not more than half of its own height, it mounts over it, and moves directly onwards, as in its natural state; but if the obstacle be equal to its own height, its progress is arrested, and the cut extremity of the body remains forced up against

the opposing substance, *the legs still continuing to move.*—If, again, the nervous cord of a Centipede be divided in the middle of the trunk, so that the hinder legs are cut-off from connection with the cephalic ganglia, they will continue to move, but not in harmony with those of the fore part of the body; being completely paralysed, so far as the animal's controlling power is concerned; though still capable of performing reflex movements by the influence of their own ganglia, which may thus continue to propel the body, in opposition to the determinations of the animal itself.—The case is still more remarkable, when the nervous cord is not merely divided, but a portion of it is entirely removed from the middle of the trunk; for the anterior legs still remain obedient to the animal's control; the legs of the segments, from which the nervous cord has been removed, are altogether motionless; whilst those of the posterior segments continue to act, through the reflex powers of their own ganglia, in a manner which shows that the animal has no power of checking or directing them.*

650. The stimulus to the reflex movements of the legs, in the foregoing cases, appears to be given by the contact of the extremities with the solid surface on which they rest. In other instances, the appropriate impression can only be made by the contact of liquid; thus a *Dytiscus* (a kind of water-beetle) having had its cephalic ganglia removed, remained motionless, so long as it rested upon a dry surface; but when cast into water, it executed the usual swimming motions with great energy and rapidity, striking all its comrades to one side by its violence, and persisting in these for more than half an hour.—Other movements, again, may be excited through the respiratory surface. Thus, if the head of a *Centipede* be cut off, and, while it remains at rest, some irritating vapour (such as that of ammonia or muriatic acid) be caused to enter the air-tubes on one side of the trunk, the body will be immediately bent in the opposite direction, so as to withdraw itself as much as possible from the influence of the vapour: if the same irritation be then applied on the other side, the reverse movement will take place; and the body may be caused to bend in two or three different curves, by bringing the irritating vapour into the neighbourhood of different parts of either side. This movement is evidently a reflex one, and serves to withdraw the entrances of the air-tubes from the source of irritation; in the same manner as the acts of coughing and sneezing in the higher animals cause the expulsion, from the air-passages, of solid, liquid, or gaseous irritating matters, which may have found their way into them.

651. From these and similar facts it appears, that the ordinary movements of the legs and wings of Articulated animals are of a 'reflex' nature, and may be effected solely through the ganglia with which these organs are severally connected; whilst in the perfect being they are harmonised, controlled, and directed by impulses which act through the *cephalic* ganglia and the nerves proceeding from them. There is strong reason to believe, that the operations to which these last ganglia are subservient, are almost entirely of a *consensual* nature; being immediately prompted by sensations, chiefly those of sight, and seldom by any processes of a truly intelligent character. When we attentively consider the habits of these animals, we find that their actions, though evidently directed to

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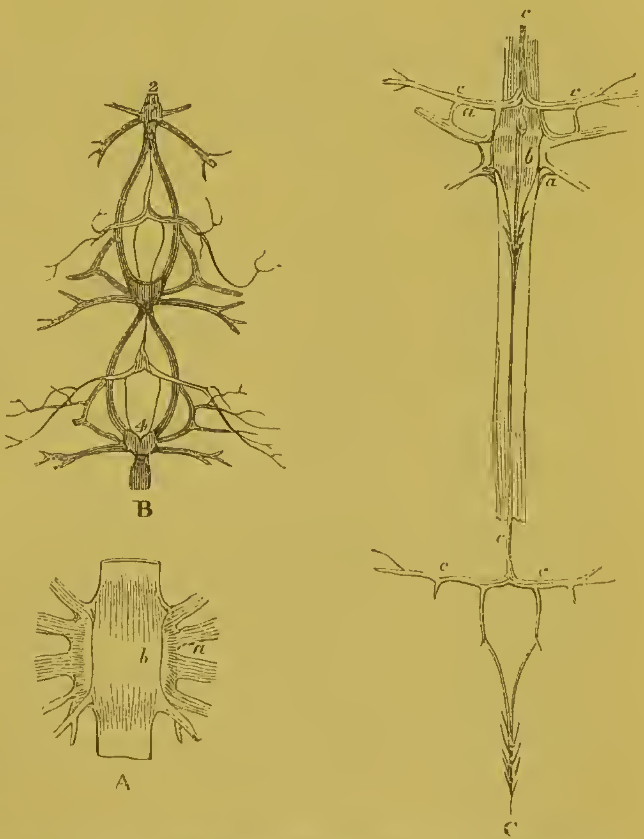
* See Newport in the "Philosophical Transactions" for 1843.

the attainment of certain ends, are very far from being of the same spontaneous nature, or from possessing the same *designed* adaptation of means to ends, as those performed by ourselves, or by the more intelligent Vertebrata, under like circumstances. We judge of this by their unvarying character,—the different individuals of the same species executing precisely the same movements, when the circumstances are the same; and by the very elaborate nature of the mental operations, which would be required, in many instances, to arrive at the like results by an effort of reason. Of such we cannot have a more remarkable example than is to be found in the operations of Bees, Wasps, and other social insects; which construct habitations for themselves, upon a plan which the most enlightened Human intelligence, working according to the most refined geometrical principles, could not surpass; but which yet do so without education communicated by their parents, or progressive attempts of their own, and with no trace of hesitation, confusion, or interruption,—the different individuals of a community all labouring effectively to one purpose, because their automatic impulses (from which their *instinctive* actions proceed) are all of the same nature. (See §§ 681, 682).

652. Not only are the locomotive ganglia multiplied in accordance with the repetition of segments and members; but the *respiratory* ganglia are multiplied in like manner, in accordance with the repetition of the respiratory organs. The respiratory division of the nervous system consists of a chain of minute ganglia, lying upon the larger cord, and sending-off its delicate nerves between those that proceed from the ganglia of the latter, as is seen in Fig. 277, C. These respiratory ganglia and their nerves are best seen in the thoracic portion of the cord, where the cords of communication between the pedal ganglia diverge or separate one from the other. And this is particularly the case in the Pupa state,

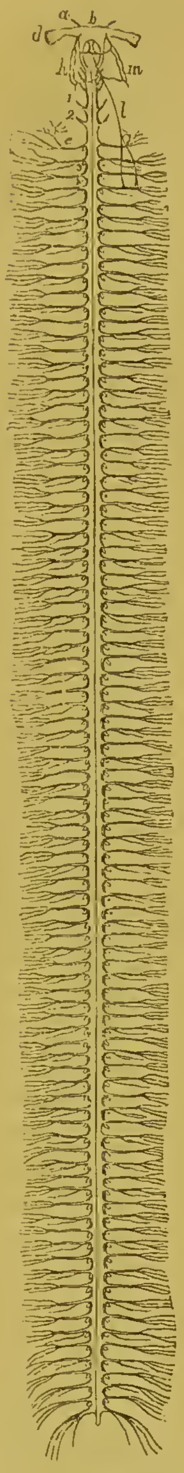
Fig. 277.



Parts of the Nervous System of Articulata.—A, single ganglion of *Centipede*, much enlarged, showing the distinctness of the purely fibrous tract *b*, from the ganglionic column, *a*:—B, portion of the double cord from the thorax of the pupa of *Sphinx ligustri*, showing the respiratory ganglia and nerves between the ganglia (2, 3, 4), and the separated cords of the locomotive system:—C, view of the two systems combined, showing their arrangement in the larva; *a*, ganglion of ventral column; *b*, fibrous tract passing over it; *c*, *c*, respiratory system of nerves distinct from both.

when the whole cord is being shortened, and their divergence is increased. The thoracic portion of the cord in the Pupa of *Sphinx ligustri,* is shown in Fig. 277, B; which represents the 2nd, 3rd, and 4th double ganglia of the ventral series, the cords of connection between them, here widely diverging laterally, and the small respiratory ganglia, which are connected with each other by delicate filaments that pass over the ganglia of the ventral cord, and which send-off lateral branches, that are distributed to the air-tubes and other parts of the respiratory apparatus, communicating with those of the other system.

FIG. 278.



Nervous System of *Iulus terrestris;*—*a,* antennal nerves; *b,* cephalic ganglia; *d,* optic nerves; *h, m,* lateral ganglia; *l,* recurrent nerve; 1, 2, 3, 4, ganglia of the ventral cord.

653. The apparatus for the ingestion and preparation of food has its own *Stomato-gastric* system of ganglia and nerves in nearly all Articulata. Thus in the *Leech,* we find a minute ganglion existing at the base of each of the three teeth (or rather jaws) by which incisions are made; these ganglia are connected with each other, and with the cephalic, by slender filaments; and they also seem to be in connection with other filaments, which may be traced along the alimentary canal. In *Iulus,* and in the larva of *Sphinx ligustri,* Mr. Newport has detected a central and two lateral ganglia, situated in close proximity with the cephalic, and communicating with them; from the former of these a 'recurrent' trunk (Fig. 278, *l*) passes backwards along the œsophagus to the stomach, apparently corresponding in its distribution with the gastric division of the par vagum in Vertebrata. The lateral ganglia (*h, m*), however, seem rather to belong to the *Sympathetic* or visceral system; their filaments being chiefly distributed upon the dorsal vessel, and upon the intestinal canal.—A more complete stomato-gastric system is found in Insects which are remarkable for their masticating powers. Thus in the *Gryllotalpa vulgaris* (mole-cricket), we find it consisting of two divisions, the *median,* and the *lateral.* The former seems to originate in a small ganglion, situated (as in the Sphinx) anteriorly and inferiorly to the cephalic mass, with which it communicates by a connecting branch on each side; from this ganglion, nerves proceed to the walls of the buccal cavity, the mandibles, &c.; but its principal trunk is sent backwards beneath the pharynx. The ramifications of this 'recurrent' are distributed along the œsophageal tube and dorsal vessel; whilst the trunk passes downwards to the stomach, where its branches inosculate with those supplied by the lateral system, and enter a pair of small ganglia, from which most of the visceral nerves radiate. The ganglia of the lateral system are two on either side, lying, one in front of the other, behind and beneath the cephalic masses, with which the anterior pair communicate:

from these, two cords pass backwards on either side, one derived from the anterior, and the other from the posterior; and these cords run along the sides of the œsophagus and dorsal vessel, and after inosculating with the branches of the median system, enter the two cœliac ganglia, whose branches radiate to the abdominal viscera.—In this, as in the preceding case, it would seem as if the *median* portion of this system partly resembles the gastric portion of the Par Vagum of Vertebrata, with the portion of the medulla oblongata which serves as its ganglionic centre; corresponding also, like the buccal ganglion of Mollusca, with the third division of the Fifth pair in Vertebrata, by which the muscles of mastication are especially supplied, and with the Glosso-pharyngeal, which is especially concerned in the act of deglutition. The union between these nerves in Fishes, near their origin, is extremely close; and they may almost be considered as proceeding from the same ganglionic centre. On the other hand, the *lateral* ganglia seem more analogous to the centres of the Sympathetic system in Vertebrata; especially in the connection of their branches with all the other systems of nerves, and in the share which they have in the formation of the cœliac ganglia. And this view of the relative functions of the two divisions included under the general term of 'stomato-gastric system,' is strengthened by the fact, that the connection between the Sympathetic system and the Par Vagum is peculiarly intimate in Fishes, so that the two sets of nerves can scarcely be isolated from each other.

654. Although the *cephalic* ganglia are usually larger than those of the ventral trunk, yet their relative size varies considerably. They receive nerve-trunks from the eyes, antennæ, and other sensory organs; and the history of their development shows that they are to be regarded as composed of several distinct pairs, which are fused (as it were) into one mass on either side. According to Mr. Newport, the cephalic ganglia of the Centipede are formed by the coalescence of the ganglia of the four segments, of which the anterior portion of the head is composed; whilst the first sub-œsophageal ganglion is in like manner composed of those of the four segments, which have coalesced to form the posterior part of the head. The relative development of the cephalic ganglia, however, is so closely accordant with that of the visual organs,—as we see, not only in comparing different species with each other, but in comparing the *larva* and *imago* states of the same Insects,—that there can be no doubt that they are to be regarded as chiefly *optic* ganglia, corresponding with the optic lobes of Fishes. There is no distinct trace, in Articulata generally, of anything that can be fairly considered homologous either with the Cerebrum or with the Cerebellum of Vertebrata; the first subœsophageal ganglion, which has been likened to the latter, being really homologous (as the distribution of its nerves abundantly proves) with the Medulla Oblongata.—(See § 682, *note*).*

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* The view here given of the Anatomical signification and Physiological action of the Nervous System of Articulated Animals, was first developed by the Author, in his Prize Thesis "On the Physiological Inferences to be deduced from the Structure of the Nervous System in the Invertebrated Classes of Animals," published in 1839. The prevalent doctrine at that period regarding the actions of the ventral cord of Articulata, was that of Mr. Newport; who maintained that the fibrous tract was *motor*, and the ganglionic *sensory*, likening them respectively to the anterior and posterior columns of the Spinal Cord. In opposition to this doctrine, the Author adduced a number of facts and argu-

655. We shall now briefly notice the principal varieties of this general plan, which are presented to us in the chief subdivisions of the Articulated series.—In its lowest forms, no other than *cephalic* ganglia (Fig. 101, *f*) have yet been detected; these give-off a band which encircles the œsophagus; and send-back a pair of longitudinal filaments that run towards the caudal extremity of the body, diverging from one another more or less widely, and giving-off branches at intervals, that encircle the body. No ganglionic enlargements have been detected in these; but it does not seem improbable that they may contain nerve-cells.—It can scarcely be doubted that a Nervous system is present in *Rotifera;* but its existence cannot yet be said to have been distinctly made-out, some of the best observers being by no means in agreement as to the structures which are to be interpreted as nerves and ganglia.*—In the *Annelida* we are led to that condition of the nervous system, which has been spoken-of as typical of the group of Articulata; for, whilst the soft-skinned species, in which there are neither organs of special sensation, nor distinct members for propulsion, have scarcely any ganglionic enlargements on the nervous cord, the higher tribes, in which the division into segments becomes distinct, and in which the animal relies for locomotion more upon the action of its members than upon that of its trunk, have ganglia regularly disposed at intervals corresponding with the division into segments. These ganglia, however, as in the inferior *Myriapoda,* in which the segments of the body are very numerous, are often so small and so closely set-together, that they seem almost to form one continuous tract (Fig. 278). The cephalic ganglia are usually of small bulk in the Annelida, in accordance with the very imperfect development of their organs of special sense; but as we pass from them to the lower Myriapoda, and thence, through the higher forms of that class, to the Insects which are most distinguished for their visual powers, we find a very remarkable increase in the relative size of these organs.—In harmony with the increased development of the sensori-motor portion of the nervous system, do we find the respiratory, stomato-gastric, and visceral centres becoming more distinct, and obviously rising in functional importance.†

656. The nervous system of *Insects,* like the rest of their organs, presents very different aspects at the different stages of their metamorphosis; and these have a peculiarly interesting relation with the

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ments, which appeared to him to prove unequivocally that the ganglia of the ventral cord are centres of 'reflex' action; and his views were very early adopted by Professors Owen, Sharpey, and other distinguished Physiologists in this country. Mr. Newport, however, having remained unconvinced, determined to re-investigate the subject for himself; and in his valuable paper in the "Philosophical Transactions" for 1843, avowed his adoption of the 'reflex' doctrine, which he strengthened by additional facts of great importance, drawn both from anatomical and from experimental inquiry.—As the Author has reason to believe that this doctrine is now generally accepted by Physiologists, both at home and abroad, as the correct interpretation of the phenomena presented by the Nervous System of Invertebrata, he has not thought it necessary to do more in this place than explain and illustrate it.

* See Huxley in "Microscopical Transactions," 2nd Ser., p. 8, and Leydig in "Kölliker and Siebold's Zeitschrift," Feb., 1852.

† In the *Amphinomidæ,* there is a remarkable gangliated chain of nerves, on each side of the abdomen, which communicates by transverse branches with the œsophageal ring and ventral column. The signification of this curious system, first discovered by Stannius ("Isis," 1831), is altogether unknown.

general characters and habits of the animals. The *Larva*, as formerly stated (§ 583), may be regarded as, in almost every respect, on a level with the Annelida; all its segments are equal, or nearly so; all are nearly alike concerned in the function of locomotion; and its nervous cords, with their ganglia, are consequently disposed with great uniformity. The number of segments being always 13 (including the head as one), that of the ganglia is usually the same; the last two or even three ganglia, however, are frequently consolidated into one. The cephalic ganglia, placed in front of the œsophagus, are small in proportion to the size they subsequently attain, in conformity with the low development of the organs of special sensation. Throughout the whole column of the larva, the separation of its lateral halves is evident; and this is a character peculiar to the lower Articulated tribes; for, in the perfect Insects, Crustacea, &c., these divisions approximate so closely, as to leave no space between them. The small respiratory filaments are seen to come-off a little above the ganglionic nerves; and these are distributed to the stigmata, and to the muscles concerned in respiration, whilst the latter ramify on the general surface and supply the locomotive organs. When the larva is about to assume the Pupa state, a very remarkable series of changes takes place in the nervous system; for the ganglia are rapidly approximated, in accordance with the sudden diminution in the length of the body; but the cords themselves are not yet shortened, so that they assume a sinuous form, and in the thoracic region the lateral halves are more widely separated than before (Fig. 277, B). No great change is yet seen in the ganglia themselves; but the œsophageal ring is much contracted; and the filaments proceeding to the rudimentary wings, which now make their appearance, begin to attain a considerable size.—The *Sphinx ligustri* remains for several months in the *Pupa* state; and the progressive alterations in its nervous system may, therefore, be very advantageously watched. It appears that, between the time of the first and that of its second metamorphosis, very considerable changes gradually take place, which all tend towards its final development. In what may be regarded as its characteristic form in the pupa state, the inter-ganglionic cords have adapted themselves to the shortened dimensions of the body, and they lie straight as in the larva; the cephalic ganglia have greatly increased in size, and are in such close proximity with the first ganglion of the trunk, that the œsophageal aperture is now much contracted; the second and third ganglia of the trunk, from which the nerves pass to the wings, are considerably enlarged, whilst the fourth and fifth have coalesced into one mass, to which the sixth also closely approximates; the abdominal columns are but little altered, their ganglia, however, are now somewhat smaller in proportion to the rest.—These changes conduct us towards the condition of the nervous system in the *Imago* or perfect Insect. The cephalic ganglia have now undergone an enormous increase (Fig. 57, *k*), the part connected with the eyes being particularly enlarged; and they extend over the œsophageal canal so much as to conceal it, uniting themselves closely with the first ganglion of the trunk. The second ganglion (*l*) has entirely shifted its position, and receded towards the middle of the thorax; the third has quite disappeared, seeming to have coalesced in part with the second, and in part with the one below it, as well as with their connecting cords. The next ganglion (*m*) appears to contain the nervous matter,—not only of the fourth and fifth which have evidently coalesced to form it,—but of the sixth and seventh, which have become obliterated, though their nerves are still given-off from the cord. The remaining ganglia have undergone but little change, but are much smaller in proportion to the rest. This alteration is evidently conformable to that which has taken place in the condition of the locomotive apparatus; all the legs, whose number is reduced to six, now proceeding from the three segments of the thorax, with which the wings also are connected.

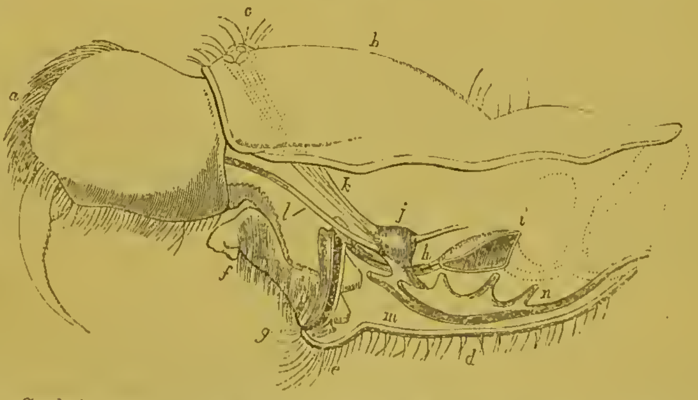
657. We see, then, that the tendency of the metamorphosis is to concentrate the ganglionic portion of the nervous system in the head and thorax; the former being the position of the organs of special sensation, the latter the situation of the locomotive apparatus. A lateral concentration may be frequently observed, as well as the longitudinal one; for whilst in some Larvæ the two cords are quite distinct, and are separated by a considerable interval, these approximate in the Imago into a single column. There are many insects in which the concentration is carried much further, than in the instance now described; the abdominal ganglia being almost entirely obliterated, and the nervous centres restricted to the head and thorax. This is partly the case in the *Melolontha* (Cockchafer), whose thorax contains three contiguous ganglionic masses, from which nerves radiate to the wings and legs, and others pass backwards into the abdomen, where no ganglia exist. The greatest concentration exists, however, in the orders *Homoptera* and *Hemiptera.*—It is interesting to observe that in many *Lepidoptera* and *Hymenoptera,* which are remarkable for rapid and powerful flight, the nerves supplying both pairs of wings are united at their origins. On the other hand, in many Insects which are not remarkable for velocity or equability of motion, the nerves supplying each wing originate separately, and have little communication, just as in the larva of the Sphinx; and in the *Coleoptera,* in which the upper pair or *elytra* are motionless during flight, the nerves frequently remain entirely separate. Hence it is not unfairly argued by Mr. Newport, that this common origin of the nerves is subservient to the uniformity and the equability of the actions of the wings, required in Insects of rapid and powerful flight. This arrangement reminds us, on the one hand, of the circular trunk that connects the nerves of the arms of Octopus (§ 646); and on the other, of the plexiform arrangement of the nerves of the extremities in the higher Vertebrata.

658. The condition of the Nervous System in *Crustacea* presents a regular series of gradations, between the type on which it is constructed in the Annelida and Myriapoda, and one of higher concentration than exists in any Insect. The former is seen in those, whose bodies display the greatest equality of segmental division, and in which there is the greatest similarity in the endowments of the several members; for in such we find the ganglia of the ventral cord corresponding in number with the segments of the body, nearly equal to each other in size, and placed at uniform distances one from another; and in *Talitrus* we find the distinctness of the two lateral halves unusually obvious, the two strands of the ventral cord being separate along their whole length, each having its own series of ganglia, and the ganglia which are thus arranged in pairs in the successive segments being connected transversely by commissural bands. In the genus *Astacus* (lobster and cray-fish), on the other hand, we find

(as in Insects) the thoracic ganglia developed to a greater size than those of the abdomen, that the locomotive members may receive their due supply of nervous influence; but as the tail is a powerful swimming organ in these animals, the difference is not so great as it would have been if the thoracic members had been the sole instruments of locomotion; and we find the last ganglion, situated above the anus, and radiating nerves to the swimming plates of the tail, particularly large, being apparently made-up by the coalescence of the sixth and seventh abdominal ganglia. In *Palemon* (prawn) and *Palinurus* (rock-lobster) we find a coalescence of the thoracic ganglia into a long elliptical perforated nervous mass; but this coalescence reaches its greatest degree in the Crab, in which all the ganglia of the ventral cord are blended into one large oval ganglion, with a perforation in its centre, which is situated near the middle of the under surface of the body, and from which nerves radiate to all parts of the trunk, to the legs, and to the short tail. The relative development of the cephalic ganglia varies with that of the organs of sense and motion which are situated in the head. They usually appear to be made-up of those of the four anterior segments of the head, from which proceed nerves that connect them with the eyes, the two pairs of antennæ (the second containing the organ of hearing), and the mandibles; whilst those of the two posterior segments ordinarily coalesce with the first ganglion of the ventral cord, to form the great sub-œsophageal ganglion, whence proceed the nerves to the feet-jaws. There is not, as in Insects, a distinct system of respiratory nerves, these being blended with those of the general sensori-motor apparatus; but the 'stomato-gastric' system is here well developed, and its relations to the visceral system of Vertebrata become apparent.—The arrangement of the nervous system in the *Cirrhipeda* is essentially the same; its chief peculiarity consisting in the relatively small-size of the cephalic ganglia, in conformity with that low development of the organs of special sense, which is characteristic of the adult state of these animals.

659. The Nervous System of the higher *Arachnida* exhibits a yet greater degree of concentration than that of Crustacea; the cephalic ganglia being in still closer relation to the sub-œsophageal mass. The former are fused-together into a single bi-lobed ganglion (Fig. 279, *j*), lying above the œsophagus (*h*), a little behind the mouth; this is connected anteriorly with the eyes (*c*) by as many nerves (*k*) as there are ocelli; and it sends-off two great nerves (*l*) to the

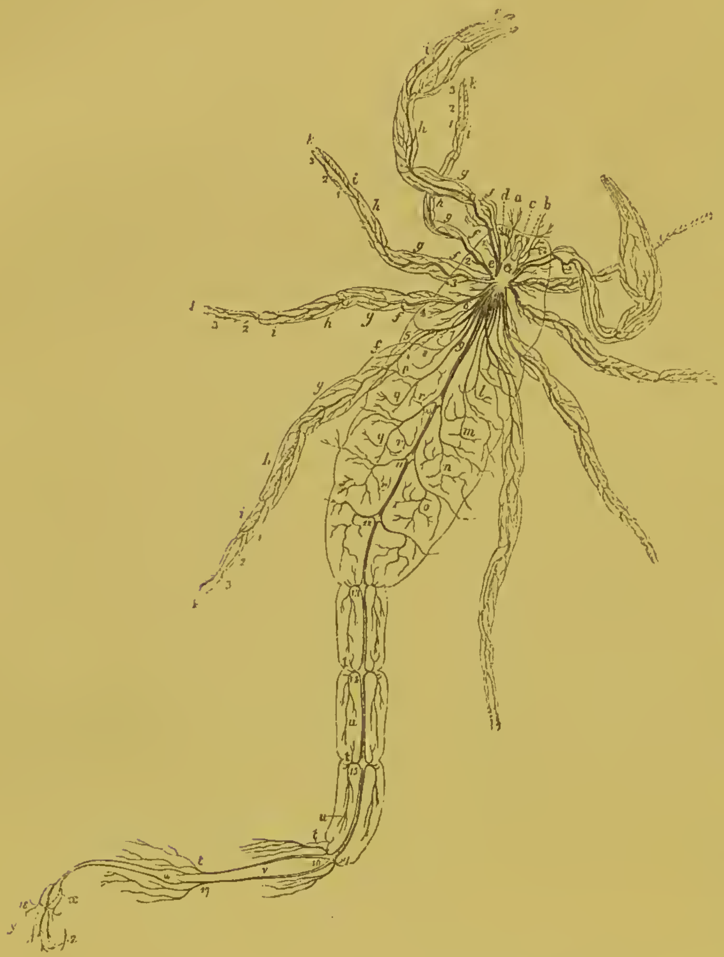
Fig. 279.



Cephalo-thorax of *Mygale*, viewed from the left side and considerably enlarged;—*a*, mandible; *b*, carapace; *c*, eyes; *d*, section of plastron; *e*, section of lip; *f*, camerostoma; *g*, entrance to the mouth; *h*, œsophagus; *i*, commencement of stomach; *j*, cephalic ganglion, receiving the optic nerves, *k*, and sending off the mandibular nerve, *l*; *m*, great thoracic ganglion; *n*, its terminal cord.

mandibles; whilst beneath, it gives off two peduncles, which closely embrace the œsophagus (*h*) and connect it with the great stellate mass (*m*), which is formed by the fusion of all the thoracic ganglia. From this mass, five pairs of nerves are given off on each side; the first to the maxillæ and their great palpi, and the remainder to the four pairs of legs; whilst posteriorly, a double cord (*n*) is sent backwards towards the abdomen, where it soon subdivides (like a 'cauda equina') into a bundle of nerves, which radiate to the several parts of the abdominal mass. In *Mygale*, an additional small ganglion is found upon the cord, anteriorly to its subdivision; but this seems to be wanting in other Spiders. — In *Scorpions*, however, the nervous system is less concentrated, as might be anticipated from the prolongation and the more complete segmentation of their bodies; and it bears somewhat the same relation to that of Spiders, that the nervous system of the Macrourous Decapods bears to that of the Brachyourous (§ 658). The ganglia of the thoracic and of part of the abdominal region coalesce into one stellate mass (Fig. 280, *e*), as in Spiders; and this supplies the thorax and its members, and the anterior portion of the abdomen, including the pulmonary branchiæ; the ventral cord of the posterior part of the abdomen, however, has ganglia of its own (Fig. 280, 10-16), which are very small in its caudal prolongation. The general dis-

Fig. 280.

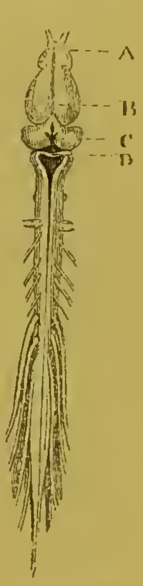


Nervous system of *Androctonus* (Scorpion):—*a*, antennal nerves; *b*, cephalic ganglia; *c*, principal optic nerves; *d*, lateral ocelli and nerves; *e*, subœsophageal ganglion; *f*, coxa; *g*, femur; *h*, tibia; *i*, basal joint of tarsus; 2, 3, second and third joints; *k*, terminal nerves to double claw; *l*, *m*, *n*, *o*, nerves to abdominal branchiæ; *p*, *q*, *r*, *s*, nerves to the segments; *t*, *u*, nerves of the caudal ganglia; *v*, terminal nerves; *w*, fifth joint of tail; *x*, anal collar; *y*, *z*, termination of the cord in the extremity of the sting; 1 to 9, nerve-trunks from the great subœsophageal ganglion; 10 to 16, ganglia of the ventral cord.

tribution of the nerves proceeding from these ganglia will be seen in the accompanying figure.*

660. Proceeding now to the *Vertebrated* series, we find, as heretofore pointed out, that their Nervous System constitutes a far more important portion of the entire organism, than it does in any Invertebrated animal; and that, in its most characteristic forms, it combines the locomotive centres of the Articulata with the sensorial centres of the Mollusca; possessing in addition two organs, the *Cerebrum* and *Cerebellum*, to which nothing distinctly analogous can be detected in any of the inferior classes.—That which may be regarded as the fundamental portion of the nervous system in Vertebrata, is the *Cranio-Spinal Axis;* which consists of the *Medulla Spinalis* or *Spinal Cord*, of its anterior prolongation termed the *Medulla Oblongata*, and of the chain of *Sensory Ganglia* which forms the superior continuation of the latter. The whole of this axis lies *above* the alimentary canal; and there is consequently no œsophageal ring, like that of Articulated and Molluscous animals; but the two lateral strands of the cranio-spinal axis still diverge from each other as they enter the cranium, so as to leave the space which is termed the *fourth ventricle* (Fig. 281). This cavity communicates anteriorly with the *third* ventricle, which separates the lateral halves of the anterior portion of the sensorial apparatus; and posteriorly with the spinal canal, which intervenes between the two lateral halves of the spinal cord. This last, however, like the space between the lateral halves of the ventral cord in the higher Articulata, is nearly obliterated in Man and the Mammalia, although sufficiently distinguishable in Fishes.—The Spinal Cord consists of a continuous tract of grey matter, enclosed within strands of longitudinal fibres; and it may thus be regarded as analogous to the ganglionic chain of the Articulata. Below the medulla oblongata, its endowments appear nearly similar throughout; for all the nerves which proceed from it are distributed to the sensory surfaces and to the locomotive organs. In some Vertebrata, whose form resembles that of the Articulata (such as the Eel and Serpent), there is no difference in the size or distribution of the several pairs of nerves, as no extremities are developed; but in other cases, the size of the trunks proceeding to the anterior and posterior extremities is much greater than that of the nerves given-off from the other segments of the cord; and the quantity of grey matter at their roots is correspondingly increased. In these trunks, both afferent and efferent fibres are bound

FIG. 281.



Nervous Centres in *Frog:*—A, olfactive ganglia; B, cerebral hemispheres; C, optic ganglia; D, cerebellum, so small as not to cover the fourth ventricle.

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* In addition to Mr. Newport's Memoirs already referred to, the following original contributions may be named as furnishing much valuable information on the Nervous System of the Articulata:—De Quatrefages, 'Sur le Syst. Nerv. des Annélides,' in "Ann. des Sci. Nat.," 3^{e} Sér., Zool., Tom. II., XIII., XIV., XVIII.; Blanchard, 'Sur le Syst. Nerv. des Insectes,' Op. cit., Tom. V.; Müller 'Dem Nervus Sympathicus analoges Nervensystem der Eingeweide bei den Insecten,' in "Nova Acta Nat. Curios." Tom. XIV.; Brandt 'Beobachtungen über die Systeme der Engeweidenerven der Evertebraten,' in "Müller's Archiv.," 1836, and "Ann. des Sci. Nat.," 2^{de} Sér., Zool., Tom. V.; and Burmeister, "Manual of Entomology," translated by Shuckard, § 190.

up; but they separate at their roots, or junction with the spinal cord,—the afferent being connected with the side of the cord nearest the surface of the back,—and the motor with that next the viscera. Both these roots have two sets of connections; some of each enter the grey substance of the cord, in which they seem lost; whilst others are continuous with the fibrous portion of the cord, and are thus put in connection either with other segments or with the encephalic centres. In this respect, then, there is a precise correspondence between the spinal column of Vertebrata and the ventral cord of Insects; and in the former, as in the latter, does experiment indicate, that each segment of the cord has a certain degree of independence; reflex actions being excitable through it, so long as the circle of afferent and motor nerves, and their ganglionic centre, are in an active and uninjured state, even though it be completely separated from all the rest.—At the upper portion of the spinal cord, however, there is a series of ganglionic enlargements, having several distinct functions. From the Medulla Oblongata proceed the chief nerves which are subservient to the respiratory actions, and also those concerned in mastication and deglutition; so that this may be regarded as combining the respiratory and the stomato-gastric ganglia.—Above or in front of this again, we find Auditory, Optic, and Olfactive ganglia, corresponding to the various subdivisions of the cephalic ganglia in the Invertebrata; these receive trunks from their respective organs of sensation, and may probably be regarded as *sensorial* centres, or seats of consciousness for the impressions which they severally transmit. The 'cranio-spinal axis' constitutes the whole nervous system of *Amphioxus*, in which there seems nothing that in the least represents a Cerebrum or Cerebellum; and among the *Cyclostome* Fishes generally, the condition of this apparatus is but little higher, save as regards the larger development of the sensory ganglia.

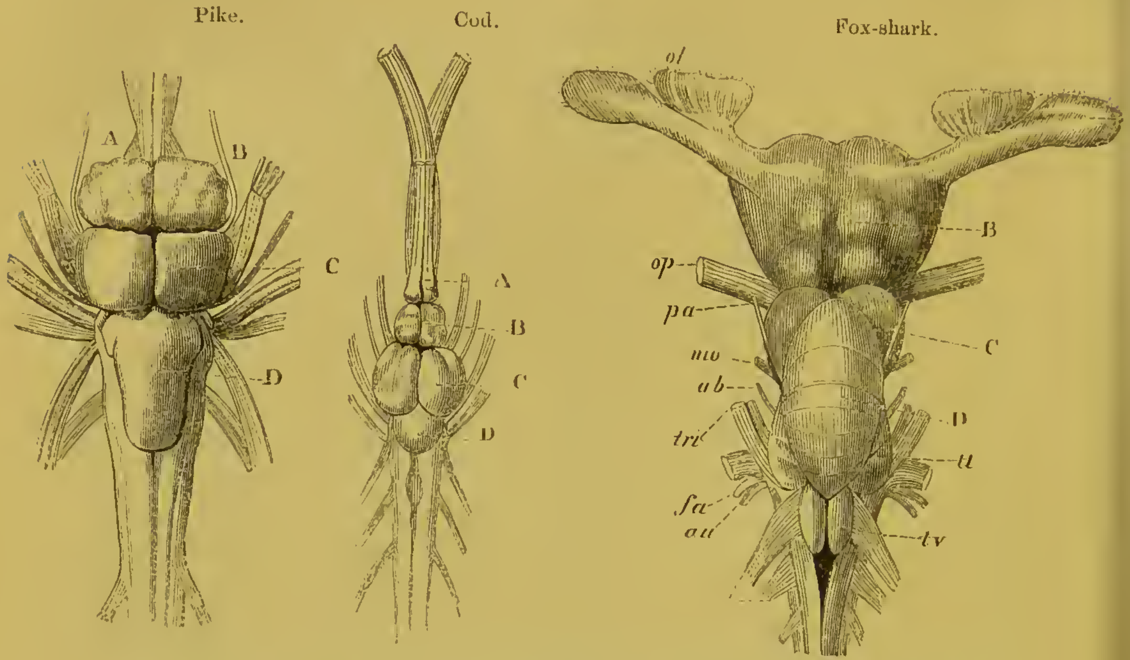
661. But in all higher Vertebrata, we find superimposed (as it were) upon the Sensory ganglia, the bodies which are known as the *Cerebral Hemispheres* or *Ganglia;* whilst superimposed upon the Medulla Oblongata, we find the *Cerebellum.* The former constitute the mass of the Brain in the Mammalia; covering-in and obscuring the sensory ganglia so completely, that the fundamental importance of these is by no means generally recognised. In Fishes, however, the proportion between the two sets of centres is entirely reversed, the rudiments of the cerebral hemispheres being usually inferior in size to the optic ganglia alone. The intermediate classes present us with a succession of gradations from the one type to the other, as regards not merely the size of the Cerebrum, but also its complexity of structure; and a very close relation may be seen between the degree of development which it exhibits, and the degree of *Intelligence* of the species. It is a point which is especially worthy of note, that no sensory nerves terminate directly in the Cerebrum, nor do any motor nerves issue directly from it; and there seems a strong probability, that there is not (as was formerly supposed) a direct continuity between any of the nerve-fibres distributed to the body, and the medullary substance of the Cerebrum. For whilst the nerves of 'special' sense have their own ganglionic centres, it cannot be shown that the nervous fibres of 'general' sense, which either enter the cranium as part of the cephalic nerves, or which pass-up from the cranio-spinal axis, have any higher

destination than the ganglionic masses termed *Thalami Optici*, which undoubtedly form part of the group of sensorial centres. So, the motor fibres which pass-forth from the cranium, either into the cephalic nerve-trunks, or into the motor columns of the spinal cord, cannot be certainly said to have an origin higher than the *Corpora Striata;* which, like the Thalami, are most assuredly to be regarded as ganglionic centres, possessing considerable independence of the Cerebrum, though formerly regarded as mere appendages to it. And we shall find strong physiological ground for the belief, that the Cerebrum has no communication with the external world, otherwise than by the sensori-motor apparatus which ministers to the automatic actions; receiving through the sensory ganglia that consciousness of external objects and events, which is the spring of its intellectual or emotional operations; and communicating its voluntary determinations to the motor part of the same system, to be worked-out (so to speak) by it, through the instrumentality of the muscles upon which it plays.—The *Cerebellum*, in like manner, presents a great difference in relative development in the several classes of Vertebrata; being in the lowest a mere thin lamina of nervous matter on the median line, only partially covering-in the 'fourth ventricle'; whilst in the highest it is a mass of considerable size, having two lateral lobes or hemispheres, in addition to its central portion. It is connected with both the anterior and the posterior columns of the spinal cord; and experiment leads to the belief, that its chief office is to combine the individual actions of different members, into the complex and nicely-balanced movements required for progression of various kinds, and, in Man, for the execution of the various operations which his intelligence prompts him to undertake.—We shall now briefly glance at the relative development and position of these parts, in the different classes of Vertebrata.

662. Commencing with *Fishes*, we find a series of four distinct ganglionic masses, arranged in a line which is nearly continuous, from behind forwards, with that of the Spinal Cord; of these, the posterior is usually single and on the median plane, whilst the others are in pairs.—1. The posterior (Fig. 282, D), from its position and connections, is evidently to be regarded in the light of a *Cerebellum;* and it bears a much larger proportion to the rest, in this class, than in any other.—2. The pair in front of this (C) are not the hemispheres of the Cerebrum, as their large size in some instances (the Cod, for instance) might lead us to suppose; but they are immediately connected with the Optic nerves, which, in fact, terminate in them; and they are therefore to be considered (like the chief part of the cephalic masses of Invertebrated animals) as *Optic lobes* or *ganglia.* They seem, however, in some degree to represent also the *Thalami Optici* of higher animals, as will be seen in the next paragraph. —3. In front of these (B) are the bodies usually considered as representing the *Cerebral Hemispheres;* which are small, generally destitute of convolutions, and possessing no ventricle in their interior,—except in the Sharks and Rays, in which they are much more highly developed than in the Osseous fishes. In the latter, in fact, these bodies seem to be the homologues of the portion of the mass lying *beneath* the ventricle in the higher Cartilaginous fishes, which is obviously the representative of the *Corpus Striatum;* so that, among ordinary Fishes, there is little or no trace of the true *Cerebrum* or Hemispheric ganglion, which makes its

first appearance in the tribe most distinguished by the elevation of its general structure.—4. Anterior to these is another pair of ganglionic

Fig. 282.



Brains of *Fishes*:—A, olfactive lobes or ganglia; B, cerebral hemispheres; C, optic lobes; D, cerebellum;—*ol*, olfactory nerve; *op*, optic nerve: *pa*, patheticus; *mo*, motor oculi; *ab*, abducens; *tri*, trifacial; *fa*, facial; *au*, auditory; *vag*, vagus; *tt*, tubercles or ganglia of the trifacial; *tv*, tubercles of the vagus.

enlargements (A), from which the Olfactory nerves arise; and these are, therefore, correctly designated as the *Olfactive ganglia.* In some instances, these ganglia are not immediately seated upon the prolonged spinal cord, but are connected with it by long peduncles; this is the case in the Sharks; and we are thus led to perceive the real nature of the portion of the trunk of the Olfactory nerve in Man, which lies within the cranium, and of its bulbous expansion on the ethmoid bone.—Besides these principal ganglionic enlargements, there are often smaller ones, with which other nerves are connected. Thus, in the Shark, we find a pair of tubercles of considerable size, at the origin of the Trifacial nerves; and another pair, in most Fishes, at the roots of the Vagi. In some instances, too, distinct *Auditory ganglia* present themselves; as in the Carp.—The Spinal Cord differs much in its proportions in different tribes of this class. In the Eel and other Vermiform fishes, it is of nearly uniform size throughout; and, in the lowest of these, the cephalic ganglia are scarcely more prominent than are those of the leech or caterpillar. In proportion as distinct locomotive members are developed, do we find enlargements of the spinal cord corresponding with the origins of their nerves, just as in the ganglionic column of Insects; and where the anterior members are very powerful, as in the *Trigla* (gurnard), these enlargements have an evidently ganglionic character. In such species as the *Lophius* (frog-fish), in which the nutritive system is enormously developed at the expense of activity of locomotion, and the animal is thus constructed more upon the Molluscous type, the nervous centres are confined to the neighbourhood of the head; for the true spinal cord soon separates into a bundle of nerves, or 'cauda equina,' which act only as conductors.

663. Although the Optic Lobes of Fishes are chiefly to be compared with the Tubercula Quadrigemina, which are the real ganglia of the Optic nerves in higher Vertebrata, their analogy is not so complete to these bodies in the fully-formed Brain of Man, as it is to certain parts which occupy their place at an earlier period. The 'third ventricle,' which is quite distinct from the Corpora Quadrigemina, is hollowed-out, as it were, from the floor of the Optic Lobes of Fishes, and the 'anterior commissure' bounds its front; hence these must be considered as analogous to the Thalami Optici and parts surrounding the third ventricle, as well as to the Corpora Quadrigemina. This is made evident by the fact, observed by Müller, that, in the Lamprey, the Optic Lobes of other Fishes are represented by two pairs of ganglionic centres; the one, which encloses the third ventricle, being the homologue of the Thalami Optici of higher animals; and the other, in which the optic nerves chiefly terminate, being the representative of their Corpora Quadrigemina. With this condition, the early state of the Brain in the embryo of the Bird and Mammiferous animal, and even in Man himself, bears a very close correspondence. The Encephalon consists at this time of a series of vesicles, arranged in a line with each other (Fig. 269); of which those that represent the Cerebrum are the smallest, whilst that which represents the Cerebellum is the largest. The latter (or *Epencephalon*), as in Fishes, is single, covering the fourth ventricle on the dorsal surface of the Medulla Oblongata. Anterior to this, is the single vesicle of the Corpora Quadrigemina (or *Mesencephalon*), from which the Optic Nerve chiefly arises; this has in its interior a cavity, the ventricle of Sylvius, which exists even in the adult Bird, where the Corpora Quadrigemina are pushed from each other, as it were, by the increased development of the Cerebral hemispheres. In front of this is the vesicle of the Third Ventricle (or *Deutencephalon*), which contains also the Thalami; as development proceeds, this, like the preceding, is covered by the enlarged hemispheres; whilst its roof becomes cleft anteriorly on the median line, so as to form the anterior entrance to the cavity. Still more anteriorly is the double vesicle (or *Prosencephalon*), which represents the hemispheres of the Cerebrum; this has a cavity on each side, the floor of which is formed by the Corpora Striata. The cavity of the cerebral vesicles has at first no opening, except into that of the third ventricle; at a later period is formed that fissure on the interior and posterior side, which (under the name of the fissure of Sylvius) enables the membranes enveloping the brain to be reflected into the lateral ventricles. —Thus it will be seen that the real analogy between the brain of the Human fœtus, and that of the adult Fish, is not so close as, from the resemblance in their external form, might have been supposed. In the small proportion which the Cerebral Hemispheres bear to the other parts, there is, indeed, a very close correspondence; and this extends also to the general simplicity of their structure, the absence of convolutions, and the deficiency of commissures. But there is a much nearer analogy between the *fœtal* brain of the Fish, and the *fœtal* brain of the Mammal; indeed, at the earliest period of their formation, they could scarcely be distinguished: during their advance to the permanent condition, however, *each* undergoes changes, which are so much more decided in the higher,

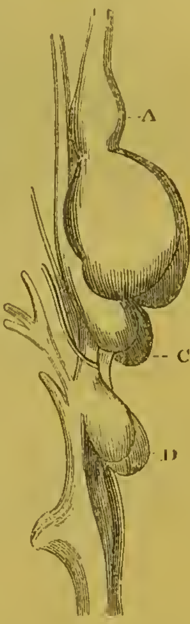
animals than in the lower, that in the latter there seems comparatively little departure from the fœtal type, whilst in the former the character of the organ appears entirely changed.

664. We have, then, in Fishes, and in the early Human embryo, this remarkable condition of the Encephalic mass,—that it is evidently made up of a series of distinct ganglionic centres, of which the portions representing the Cerebral Hemispheres are usually the smallest, being obviously an addition to the remainder, whose existence is independent of them. Thus, in passing from before backwards, we meet first with the Olfactive ganglia; 2d, with the Corpora Striata, overlaid with the mere rudiment of a Cerebrum; 3d, with the Thalami Optici, inclosing the third ventricle; 4th, with the Corpora Quadrigemina, or proper Optic Ganglia; and 5th, with the Cerebellum. Besides these, we have centres for the Auditory and Gustative nerves, or proper Auditory and Gustative ganglia, lodged in the Medulla Oblongata. All these ganglionic centres have their own distinct connections with the Medulla Oblongata; except the Hemispheres, which do not appear to communicate with it, except through the medium of the bodies on which they are superimposed. We shall probably form the most correct view of their relations, if, excluding the Cerebrum and Cerebellum, we regard them as collectively homologous with the Cephalic ganglia of Invertebrated animals, which, as we have seen, are the immediate centres of the nerves of sensation, and are connected with the ganglia in the trunk by fibrous cords which represent the Medulla Oblongata. The size of the Cephalic ganglia, in the higher Invertebrata, is chiefly dependent upon the development of the visual organs, which are the principal guides in the movements of these animals; but, as Mr. Newport's researches on their embryonic development have shown, they are really composed of several pairs of distinct ganglionic centres (§ 654); and it is interesting, also, to remark, that the situation of the rudimentary organ of hearing in the Nudibranchiate Mollusca is precisely analogous to that of the Auditory ganglion in the Vertebrata, the auditory sacculi being lodged in the posterior lobes of their cephalic ganglia. The Optic and Olfactive ganglia of Vertebrated animals receive nerves of sensation from the organs situated in their neighbourhood, and seem to give-off motor nerves in the fibrous peduncles which connect them with the motor tract of the Medulla Oblongata. The Thalami Optici and Corpora Striata, on the other hand, appear to be the ganglionic centres of fibres entirely transmitted through the Spinal Cord, as they do not directly receive or give-off any nerve-trunks, save that the former receive some of the roots of the Optic nerve; and the special connection of the former with the Sensory tract, and of the latter with the Motor, with other reasons hereafter to be given, lead to the belief that these are the ganglionic centres of 'common' or tactile sensations, and of the movements immediately excited by them; whilst the passage of some of the filaments of the Optic Nerve into the Thalami, may not improbably be interpreted as ministering to that peculiarly-intimate connection, which exists between the senses of Sight and Touch.—Thus, we may consider this series of ganglionic centres as forming, with the Spinal Cord (of which they constitute the encephalic representation), an *automatic* apparatus, exactly comparable with that of the Insect; and on this the Cerebrum is superimposed, in such a manner as to be obviously an independent organ, receiving its stimulus to action

from the sensorial centres, and transmitting its motor impulses through the same channel.

665. The Brain of *Reptiles* does not show any considerable advance in its general structure above that of Fishes; but the Cerebral Hemispheres, are usually much larger in proportion to the optic lobes; whilst the Cerebellum is smaller (Fig. 283). The very low development of the Cerebellum is especially seen in the Frog (Fig. 281), in which it is so small as not even to cover-in the 'fourth ventricle;' but it is common to nearly the whole group. The deficiency in commissures still exists to a great extent. The 'anterior commissure' in front of the 'third ventricle,' is the only uniting band which can be distinctly traced in Fishes; and Reptiles have, in addition to this, a layer of uniting fibres which may be compared to the 'fornix;' but as yet, there is no vestige of a true 'corpus callosum,' or great transverse commissure of the Hemispheres. The distinction between the tubercula quadrigemina, and the parts inclosing the third ventricle, is more obvious than in Fishes; in fact, the optic ganglia of Reptiles correspond pretty closely with the vesicle of the tubercula quadrigemina, or mesencephalon, in the brain of the fœtal Mammal.—The Nervous Centres of *Batrachia*, like all their other organs, present, in the Tadpole state, the characters of those of Fishes; and these are partly retained by the 'perennibranchiate' species during the whole of their existence. In the Frog and its allies, however, the Encephalon acquires the Reptilian type; and a marked change takes place in the condition of the Spinal Cord. For in the Tadpole condition, this organ is elongated, and of nearly uniform size throughout; but in proportion as the tail is atrophied and the extremities are developed, do we find the spinal cord relatively shortened, and presenting enlargements at the parts in which the nerves of the limbs originate, especially those of the posterior extremities. Similar enlargements are seen in Turtles, in connection with the nerves of both the anterior and posterior extremities, which take a nearly equal share in the general movements of the body. On the other hand, in Serpents, as in Eels and other snake-like Fishes, the Spinal Cord is of nearly uniform size throughout; and as it gives-off, in some instances, more than 300 pairs of nerves, it is obvious that only a very small proportion of their fibres can have any direct connection with the Encephalon, through the longitudinal strands of the Medulla Oblongata.

Fig. 283.

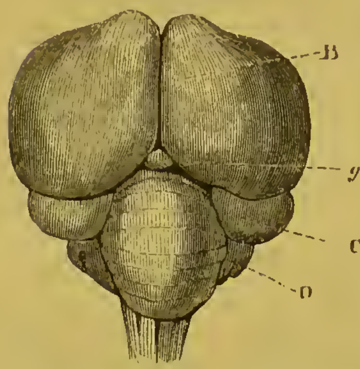


Brain of *Turtle*:—A, olfactive ganglia; B, cerebral hemispheres; C, optic ganglia; D, cerebellum.

666. In the Brain of *Birds* (Fig. 284), our attention is at once attracted by the increased development of the Cerebral Hemispheres, which extend forwards so as to conceal the Olfactive ganglia, and arch backwards so as partly to cover the Optic ganglia (here called the Corpora Bigemina), which are separated from each other and thrown to either side, being now quite distinct from the Thalami Optici. The Cerebellum also is much increased in size, proportionably to the Medulla Oblongata and its ganglia; and it is sometimes marked with transverse lines, which indicate

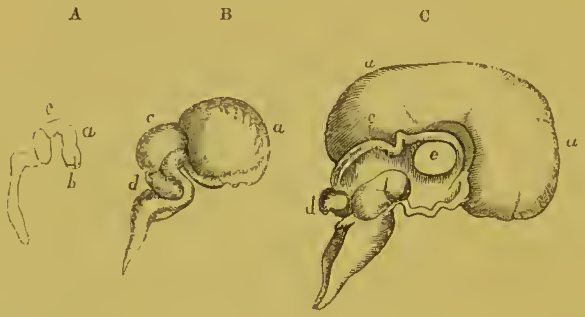
the intermixture of grey and white matter in its substance; there is as yet, however, no appearance of a division into hemispheres. On drawing-apart the hemispheres of the Cerebrum, the Corpora Striata, Optic Thalami, and Corpora Bigemina or Optic Ganglia, are seen beneath them; and their collective size still bears a considerable proportion to that of the whole Encephalon. The Optic Ganglia are still hollow, as they are in the embryo condition of Man. Indeed the Brain of the Human fœtus, about the twelfth week (Fig. 285, B), will bear comparison, in many respects, with that of the Bird. The Cerebral hemispheres, much increased in size, and arching-back over the Thalami and Optic ganglia, but destitute of convolutions, and imperfectly connected by commissures,—the large cavity still existing in the Optic ganglia, and freely communicating with the third ventricle,—and the imperfect evolution of the Cerebellum,—make the correspondence in the general condition of the two very considerable.

FIG. 284.



Brain of *Buzzard:* the olfactive ganglia are concealed beneath B, the hemispheres; C, optic ganglia; D, cerebellum; *g,* pineal gland.

FIG. 285.

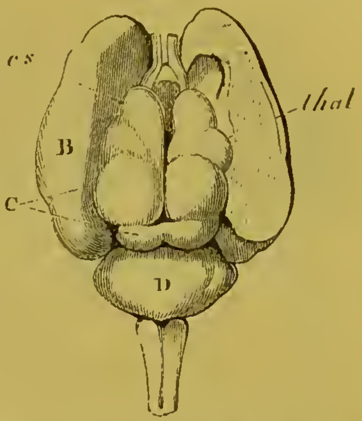


Early Stages of *Development of Human Brain;* A, at 7th week; B, at 12th week; C, at 15th week:—*a,* cerebral hemispheres; *b,* corpora striata; *c,* corpora quadrigemina; *d,* cerebellum.

667. The Brain of the lower *Mammalia* presents but a slight advance upon that of Birds, in regard both to the relative proportions of its parts, and to their degree of development. Thus, in the *Marsupialia,* the Hemispheres exhibit scarcely any convolutions; the great transverse commissure, or 'corpus callosum,' is deficient; and, as in all the Oviparous Vertebrata, the rudimentary Cerebrum represents, not the entire cerebrum of Man, but its *anterior* lobe only. There is gradually to be noticed, however, in ascending the scale, a backward prolongation of the Cerebral hemispheres, so that first the Optic ganglia, and then the Cerebellum, are covered by them; and this extension corresponds with the development of the *middle* lobe and its great commissure. The Cerebellum partly shows itself, however, in all but the Quadrumana, when we look at the brain from above downwards; in the *Rodentia* (Figs. 286, 287), which are in this respect among the lowest of the Placental Mammalia, nearly the whole of the Cerebellum is uncovered. In proportion to the

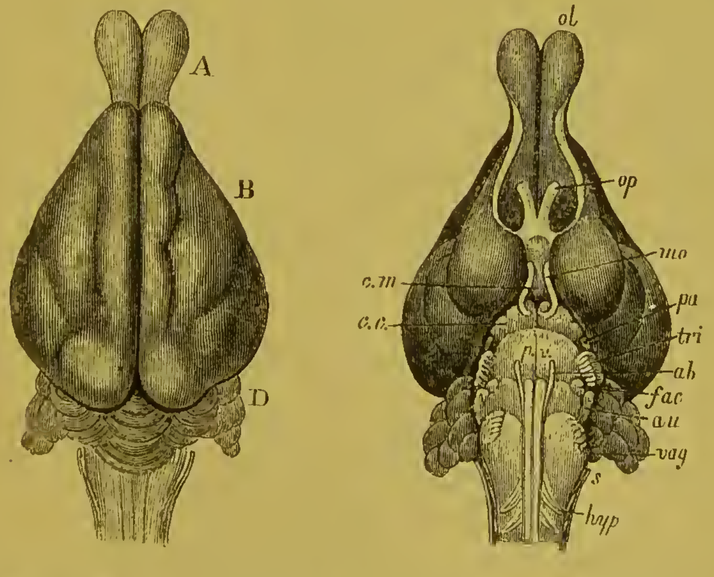
increase of the Cerebral hemispheres, there is a diminution in the size of the ganglia immediately connected with the organs of sense; and this in comparison, not only with the rest of the Encephalon, but even with the Spinal cord; so that in Man the Tubercula Quadrigemina are absolutely smaller than they are in many animals of far inferior size. The internal structure of the Hemispheres becomes more complex, in the same proportion as their size and the depth of the convolutions increase; and in Man all these conditions present themselves in a far higher degree than in any other animal. In fact, it is only among the Ruminantia, Pachydermata, Carnivora, and Quadrumana, that regular convolutions can be said to exist; and it is only in the higher Carnivora and Quadrumana, that there is any indication of the existence of *posterior* lobes; the presence of which is marked by the development of the posterior cornua of the lateral ventricles, and by the position of the hippocampus major. All these phases are distinguishable in the development of the brain of the Human embryo; for up to the end of the third month (Fig. 285, B), the hemispheres present only the rudiments of anterior lobes, and do not even cover-in the thalami; during the fourth and part of the fifth months, the middle lobes are developed on their posterior aspect, and cover the tubercula quadrigemina (Fig. 288); and the posterior lobes, of which there was no previous

Fig. 286.



Brain of *Squirrel*, laid open; the hemispheres, B, being drawn to either side, to show the subjacent parts; C, the optic lobes; D, cerebellum; *thal*, thalamus opticus; *c s*, corpus striatum.

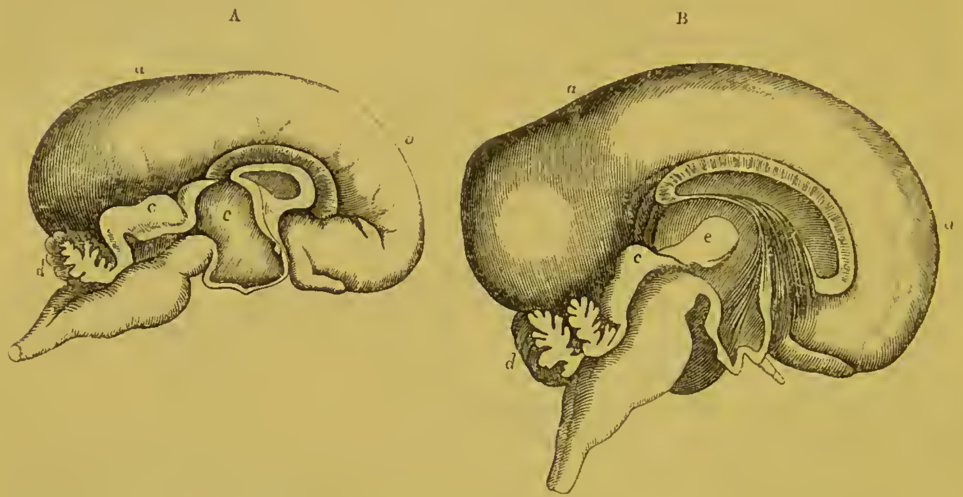
Fig. 287.



Upper and under surface of Brain of *Rabbit*, A, B, D, as before; *ol*, olfactive lobes; *op*, optic nerve; *mo*, motor oculi; *cm*, corpora mamillaria; *c c*, crus cerebri; *pv*, pons varolii; *pa*, patheticus; *tri*, trifacial; *ab*, abducens; *fac*, facial; *au*, auditory; *vag*, vagus; *s*, spinal accessory; *hyp*, hypoglossal.

rudiment, subsequently begin to sprout from the back of the middle lobes, remaining separated from them by a distinct furrow, however, even in the brain of the mature fœtus, and sometimes in that of older persons.

Fig. 288.



More advanced Stages of *Development of Human Brain;* A, at 21st week; B, at 27th week: *a*, *a*, cerebral hemispheres; *c*, corpora quadrigemina; *d*, cerebellum; *e*, thalamus opticus.

—The correspondence between the bulbous expansion of the Olfactive nerves in Mammalia, and the Olfactive lobes of the lower Vertebrata, is made evident by the presence, in both instances, of a cavity which communicates with the lateral ventricle on each side; it is in Man only, that this cavity is wanting. The external form of the Corpora Quadrigemina of Mammalia, differs from that of the Optic ganglia of Birds, owing to the division of the former into anterior and posterior eminences (the nates and testes); and there is also an internal difference, occasioned by the contraction of the cavity or ventricle, which now only remains as the 'aqueduct of Sylvius.' The Auditory ganglia are lodged in the substance of the Medulla Oblongata, forming the 'grey nuclei' of the 'posterior pyramids;' and similar nuclei in the 'restiform bodies' are the ganglionic centres of the Glosso-pharyngeal nerves, and probably minister to the sense of Taste.—The Cerebellum is chiefly remarkable for the development of its lateral parts or Hemispheres; the central portion, sometimes called the 'vermiform process,' is relatively less developed than in the lower Vertebrata, in which it forms the whole of the organ.

668. Thus, when we analyse the entire *Cerebro-Spinal* system of Vertebrata, we find that it may be resolved into the following fundamentally-distinct parts:—1. A system of ganglia subservient to the reflex actions of the organs of *locomotion*, and corresponding with the chain of pedal or locomotive ganglia that makes-up the chief part of the ventral cord of the Articulata; in this system, the grey or vesicular matter forms one continuous tract, which occupies the interior of the *Spinal Cord.*—2. A ganglionic centre for the movements of *respiration*, and another for those of *mastication* and *deglutition;* these, with part of the preceding, make up the proper substance of the *Medulla Oblongata.*—3. A series of ganglia, in immediate connection with the organs of *Special Sense;* these are

situated within the cranium, at the anterior extremity of the Medulla Oblongata; and in the lowest Vertebrata, they constitute by far the largest portion of the entire Encephalon.—4. The *Cerebellum,* which is a sort of off-shoot from the upper extremity of the Medulla Oblongata, lying behind the preceding.—5. The *Cerebral Hemispheres,* a pair of ganglionic masses, which lie upon the ganglia of special sense, capping them over more or less completely, according to their relative development.—Of these, the first three may be considered as constituting the essentially *automatic* portion of the nervous centres; whilst the Cerebrum is certainly the original source of all *voluntary* movements; and the Cerebellum seems to contribute to the adjustment and combination of the individual acts, by which the directions of the Will are worked-out, through the instrumentality of the automatic apparatus, in the manner to be presently explained.

669. The development of the *Sympathetic* or Visceral system of nerves in the Vertebrated classes, advances *pari passu* with that of the Cerebro-Spinal; from which it gradually becomes more distinct. In many Fishes, as in the Invertebrata, the two are so blended that it is difficult to separate them, the visceral nerves appearing to be derived exclusively from the cerebro-spinal system; but, as we ascend the scale, the former is seen to possess centres of its own; and in Mammalia it becomes a system of great complexity, having two large ganglia (the Semilunar) in the abdomen, from which filaments are distributed to all the digestive organs, besides a regular series along the spine. It communicates with each of the spinal nerves near their roots, as well as with most of the cerebral; and interchanges filaments with them. It forms a plexus which is minutely distributed upon the large vascular trunks, and which probably accompanies their ramifications into every part of the system.

670. It is in Vertebrated animals, that we meet with the greatest complexity in the actions of the Nervous system, and that we experience the greatest difficulty in determining the attributes of each of its parts. This is due, on the one hand, to the increased variety in its *modi operandi;* for whilst the actions of the lower tribes belong for the most part to the Automatic group, many of those of Vertebrata are dependent upon Voluntary determinations, and some upon Emotional impulses; and it is not always easy to assign their true source. On the other hand, a difficulty arises out of the peculiarity in the arrangement of their several ganglionic centres, which are for the most part combined together in one continuous mass, so that they cannot be isolated one from another without the infliction of such injuries, as must considerably interfere with the performance of their appropriate actions. Still, taking Nature as our guide, and availing ourselves of the experiments which she has prepared for us in the different natural combinations of these ganglionic centres, it seems possible to attain to very definite conclusions in regard to all the most general questions involved in the inquiry; and to these alone will it be desirable for us here to restrict ourselves.

671. The *Cranio-Spinal Axis,*—including the Spinal Cord, Medulla Oblongata, and Sensory Ganglia,—may be considered as the representative of the entire nervous system of Articulated animals (save of that portion which is homologous with the Sympathetic); and, like it, seems to be the centre of all the movements which may be designated as *automatic.*

Although it was long held as a physiological truth, that the principal part of the Sensory fibres passes-up to the grey matter which forms the surface of the Cerebral hemispheres, and that the fibres which are subservient to voluntary Motion originate in the same situation, and pass downwards through the spinal cord and nerve-trunks to the muscles; yet anatomical inquiry fails to sanction such a doctrine, and tends, concurrently with the results of physiological investigation, to the conclusion, that no sensory fibres pass upwards beyond the chain of sensory ganglia (including the thalami optici), and that no motor fibres really originate from any higher point than the corpora striata. With this chain of ganglionic centres, which constitutes the real *sensorium*, the vesicular matter of the Cerebral or Hemispheric ganglia is connected, by that vast collection of fibres which radiate from their central portion to their surface; but these fibres may be regarded as simply *commissural*, connecting the grey matter of the cerebral surface with the thalami optici, corpora striata, and other ganglionic centres, whose endowments are altogether distinct. It is, then, in the Cranio-Spinal Axis, that all the afferent and sensory nerves terminate; and it must be through it, therefore, that the Cerebrum is acted upon by external impressions. On the other hand, it is in the same Axis that all the motor nerves originate; and it must be through it, therefore, that the Cerebrum is brought into communication with the Muscular apparatus.

672. That this Cranio-Spinal Axis is a distinct centre of automatic action, and does not derive its power (as formerly supposed) from the Cerebrum, is made evident by a variety of considerations. Thus, Infants are sometimes born without any Cerebrum or Cerebellum; and such have existed for several hours or even days, breathing, crying, sucking, and performing various other movements. The Cerebrum and Cerebellum have been experimentally removed from Birds and young Mammalia, thus reducing these beings to a similar condition; and all their vital operations have, nevertheless, been so regularly performed, as to enable them to live for weeks, or even months. In the *Amphioxus*, as already stated (§ 660), we have an example of a completely-formed adult animal, in which no rudiment of a Cerebrum or Cerebellum can be detected. And in ordinary profound sleep, or in apoplexy, the functions of these organs are so completely suspended, that the animal is, in all essential particulars, in the same condition for a time as if destitute of them. It is possible, indeed, to reduce a Vertebrated animal to the condition (so far as its nervous system is concerned) of an Ascidian Mollusk (§ 640); for it may continue to exist for some time, when not merely the Cerebrum and Cerebellum have been removed from above, but when nearly the whole Spinal Cord has been removed from below,—that part only of the latter being left (namely, the Medulla Oblongata), which, being the centre of the respiratory actions, bears the greatest correspondence to the single ganglion of the Tunicata. On the other hand, no Vertebrated animal can exist by its Encephalon alone, the Spinal Axis being destroyed or removed; for the reflex actions of the latter are so essential to the continuance of its respiration, and consequently of its circulation, that if they be suspended (by the destruction of the portion of the Cord which is concerned in them), all the organic functions must soon cease.

673. That the actions performed by the Spinal Cord are of a simply

reflex nature,—consisting in the excitement of muscular movements, in respondence to external impressions, without the necessary intervention of sensation,—appears to be a necessary inference from the facts that have been brought to light by experiment and observation. Experiments on the nature of this function are best made upon cold-blooded animals; as their general functions are less disturbed by the effects of severe injuries of the nervous system, than are those of Birds and Mammals. When the Cerebrum has been removed, or its functions have been suspended by a severe blow upon the head, a variety of motions may be excited by their appropriate stimuli. Thus, if the edge of the eye-lid be touched with a straw, the lid immediately closes. If liquid be poured into the mouth, or a solid substance be pushed within the grasp of the muscles of deglutition, it is swallowed. If the foot be pinched, or burned with a lighted taper, it is withdrawn; and (if the creature experimented on be a Frog) the animal will leap away, as if to escape from the source of irritation. If the cloaca be irritated with a probe, the hind-legs will endeavour to push it away.—Now the performance of these as well as of other movements, many of them most remarkably adapted to an evident purpose, might be supposed to indicate, that *sensations* are called-up by the impressions; and that the animal can not only *feel*, but can *voluntarily* direct its movements, so as to get rid of the irritation which annoys it. But such an inference would be inconsistent with other facts.—In the first place, the motions performed by an animal under such circumstances, are never spontaneous, but are always excited by a *stimulus* of some kind. Thus, a decapitated Frog, after the first violent convulsive movements occasioned by the operation have passed away, remains at rest until it is touched; and then the leg, or its whole body, may be thrown into sudden action, which immediately subsides again. In the same manner, the act of swallowing is not performed, except when it is excited by the contact of food or liquid; and even the respiratory movements, spontaneous as they seem to be, would not continue, unless they were continually re-excited by the presence of venous blood in the vessels. These movements are all *necessarily* linked with the stimulus that excites them;—that is, the same stimulus will always produce the same movement, when the condition of the body is the same. Hence it is evident, that the judgment and will are not concerned in producing them; and that the *adaptiveness* of the movements is no proof of the existence of consciousness and discrimination in the being which executes them,—the adaptation being made *for* that being, by the peculiar structure of its nervous apparatus, which causes a certain movement to be executed in respondence to a given impression,—not *by* it. An animal thus circumstanced may be not unaptly compared to an automaton; in which particular movements, adapted to produce a given effect, are produced by touching certain springs. Here the adaptation was in the mind of the maker or designer of the automaton; and so it evidently is, in regard to the purely automatic movements of animals, as well as with respect to the various operations of their nutritive system, over which they have no control, yet which concur most admirably to a common end.

674. Again, we find that such movements may be performed, not only when the Encephalon has been removed, the spinal cord remaining entire, but also when the Spinal Cord has been itself cut across, so as to be

divided into two or more portions,—each of them completely isolated from each other, and from other parts of the nervous centres. Thus, if the head of a Frog be cut-off, and its spinal cord be divided in the middle of the back, so that its fore-legs remain connected with the upper part, and its hind-legs with the lower, each pair of members may be excited to movement by a stimulus applied to itself; but the two pairs will not exhibit any consentaneous motions, as they will do when the spinal cord is undivided. Or, if the Spinal cord be cut-across, without the removal of the Brain, the lower limbs may be *excited* to movement, by an appropriate stimulus, though they are completely paralysed to the *will;* whilst the upper remain under the control of the animal, as completely as before. And when this separation happens to be made in the Human subject by accidental injury or by disease, it is found that if it be complete, there is not only a total want of voluntary control over the lower extremities, but a complete absence of sensation also,—the individual not being in the least conscious of any impression made upon them. When the lower segment of the Cord remains sound, and its nervous connections with the limbs are unimpaired, distinct reflex movements may be excited in the limbs, by stimuli directly applied to them; as, for instance, by pinching the skin, tickling the sole of the foot, or applying a hot plate to its surface; and this without the least sensation, on the part of the patient, either of the cause of the movement, or of the movement itself.

675. This fact, taken in connection with the preceding experiments, both upon Vertebrated and Articulated animals, distinctly proves that Sensation is *not* a necessary link in the chain of 'reflex' actions of this lowest class, which may be appropriately distinguished as *excito-motor;* but that all which is required is an *afferent* fibre, capable of receiving the impression made upon the surface, and of conveying it to the centre; a *ganglionic centre,* composed of vesicular nervous substance, into which the afferent fibre passes; and an *efferent* fibre, capable of transmitting the motor impulse, from the ganglionic centre, to the muscle which is to be thrown into contraction.—These conditions are realised in the Spinal Cord. We may have reflex actions excited through any one isolated segment of it, as through a single ganglion of the ventral cord of Articulata, but they are then confined to the parts supplied by the nerves of that segment: thus, if the spinal cord of a Frog be divided just above the origin of the crural nerves, the hind-legs may be thrown into reflex contraction by various stimuli applied to themselves, while the fore-legs will exhibit no movement of this kind. But if the brain be removed, and the Spinal Cord be left entire, movements may be excited in distant parts, —as, for example, in the fore-legs, by any powerful irritation of the posterior extremities,—and *vice versâ.* This is particularly well seen in the convulsive movements which take place in certain disordered states of the nervous system; a slight local irritation being sufficient to throw almost any muscles of the body into a state of energetic action. And a similar state may be artificially induced, by applying strychnine (in solution) to the Spinal Cord of a decapitated Frog.

676. The particular 'reflex' actions to which the Spinal Cord (using that term in its limited sense, as excluding the Medulla Oblongata) is subservient, are mostly connected with the Organic functions; and they are chiefly of an *expulsive* kind, being destined to force-out the contents

of various cavities of the body. Thus the ordinary acts of defecation and urination, ejaculatio seminis, and parturition, are all reflex movements, over which the Will has but very little control, when once the stimulus by which they are excited has come into full action.—But the movements of the posterior extremities are occasionally due to the purely-automatic action of the Spinal Cord. It has been already noticed that these may be excited, even in Man, when the spinal cord has been severed in the middle without injury to its lower segment; and it is remarkable that gentle stimuli, applied to the skin of the sole of the foot, appear the most capable of producing them. We have seen how completely, in the lower animals, the acts of progression may be sustained, by the repeated stimulus of the contact of the ground, or of fluid, without any influence from the Cephalic ganglia; the power of these being limited, it would seem, to the control and direction of them. And there is strong reason to believe, that, so far as the ordinary acts of locomotion are concerned, the movements of the inferior extremities in Man may be performed on the same plan; being continued by the 'reflex' power of the Cord, when once set in action by the Will, whilst we are walking steadily onwards; the mind being at the same time occupied by some train of thought, which engrosses its whole attention (§ 684). Even when the mind is sufficiently on the alert to guide, direct, and control the motions of the limbs, their separate actions appear to be performed without any direct agency of the will. It is certain that, in Birds, the movements of flight may be performed after the removal of the Cerebrum (§ 678).

677. The *Medulla Oblongata* does not differ in any other essential particular from the Spinal Cord (of which it may be considered as the cranial prolongation), than this; that whilst the ganglionic portion of the latter is made-up of the centres which minister to general locomotion, being homologous with the repetition of the *pedal* ganglia in the ventral cord of Articulated animals, the former contains the centres of the movements of Deglutition and Respiration, and may therefore be regarded as representing their *stomato-gastric* and *respiratory* ganglia.—Both these actions are purely 'automatic' in their character; and the Will can only restrain them, when the stimulus which calls them forth is not acting with any great degree of potency. The act of *Swallowing* is excited by the contact of solid or fluid matters with the membrane lining the fauces; and the impression, conveyed to the Medulla Oblongata by an afferent nerve (the 'glosso-pharyngeal'), excites there a reflex impulse, which, being transmitted along a motor nerve (chiefly the pharyngeal portion of the 'par vagum') to the muscles, calls them into those combined and consecutive movements, which are requisite for the reception of the food from the buccal cavity, and for its propulsion down the œsophagus. These movements may be excited in a state of complete unconsciousness; or after the removal of the Cerebrum from above, and of the Spinal Cord from below. And when we suppose that we are swallowing *voluntarily*, the action of the Will is limited to the mere excitation of the reflex movement, by the carrying-back of the solid or liquid to be swallowed, upon the tongue, into contact with the lining membrane of the fauces. When this contact has once been effected, scarcely any power of the will could prevent the consecutive movement. The acts of *Prehension* of food with the lips, though usually effected by voluntary power in the adult, seem to

be capable of taking-place as a part of the reflex operation of the Medulla Oblongata, in the Human infant, as in the lower animals. This is particularly evident in the prehension of the nipple by the lips of the infant, and in the act of suction which the contact of that body (or of any resembling it) seems to excite. The experiments provided for us by nature, in the production of anencephalous monstrosities, fully prove that the integrity of the nervous connection of the lips and respiratory organs with the Medulla Oblongata, is alone sufficient for the performance of this action; and experiments upon young animals, from which the brain has been removed, establish the same fact. Thus Mr. Grainger found that, upon introducing his finger, moistened with milk, or with sugar and water, between the lips of a puppy thus mutilated, the act of suction was excited; and not merely the act of suction itself, but other movements having a relation to it; for as the puppy lay on its side, sucking the finger, it pushed-out its feet, in the same manner as young pigs exert theirs in compressing the sow's dugs. The act of *Mastication*, again, although usually considered a voluntary one, comes by habit to be performed without any exertion of the will; and may then be referred to that class denominated 'secondarily automatic' (§ 684).—The movements of *Respiration* are purely 'reflex' in their character, although capable of being imitated, or to a certain extent controlled, by an exertion of the Will. The purpose of this subjection, which seems peculiar to the higher animals, is evidently to render them subservient to the production of Vocal Sounds; to which they obviously could not minister, if they were as independent of voluntary control and direction, as they seem to be in the lower animals. But this subjection only exists, when the stimulus does not act with more than moderate force, that is, when the blood is undergoing its normal aeration; for if the process be checked for a few seconds, the demand for aeration becomes so strong, that the Will can no longer restrain the movement to which it prompts. The stimulus to this action chiefly originates in the lungs, and is either the presence of venous blood in their capillaries, or of carbonic acid in their air-cells. This impression (which need not be strong enough to arouse the consciousness) is conveyed to the Medulla Oblongata by the pulmonic portion of the 'par vagum'; and a reflex impulse is then transmitted through the 'phrenic' and 'intercostal' nerves, to the diaphragm and the muscles of the ribs, which produces the act of inspiration. It is not through the 'par vagum' alone, however, that excitor impressions are conveyed; for the nerves of the general surface, and especially of the face, are subservient to this function; and it is through them that the *first* inspiration is excited, by the contact of cold air with the skin of the new-born Mammal. It appears, too, that the Cerebrum is concerned in the maintenance of the respiratory movements, not volitionally, however, but automatically; the circulation of imperfectly-arterialised blood through its vessels, occasioning an impulse to be transmitted from it to the respiratory nerves, through the medium of their ganglionic centre. So when the respiratory efforts are very powerfully called-forth, various other parts of the nervo-muscular apparatus are put in action, besides those just mentioned.

678. The chain of *Sensory Ganglia*, which forms nearly the entire Encephalon of Fishes (§ 662), but which is overlaid and obscured in Man

and the higher Vertebrata by the relatively-enormous development of the Cerebrum, may be regarded as constituting the true *Sensorium;* that is, as the seat of *consciousness*, to which impressions made upon the nerves of sense are carried, and through which the individual is rendered cognisant of them. There is abundant evidence that this endowment does not exist in the locomotive, stomato-gastric, or respiratory ganglia, of which the Spinal Cord and the principal part of the Medulla Oblongata are made-up; whilst on the other hand, there is adequate proof that the presence of a Cerebrum is not necessary to its possession. For these ganglia are obviously homologous with the Cephalic ganglia of Invertebrated animals; and if the latter be the instruments of consciousness and the seat of sensibility (to deny which, would be to refuse these endowments to Invertebrated animals altogether), there is no reason to doubt that the former are so likewise, their relations to the nerves of sense being precisely the same. There is no adequate reason for the belief, that the addition of the Cerebral Hemispheres, in the Vertebrated series, *alters* the endowments of the Sensory Ganglia on which they are superimposed; on the contrary, we have everywhere seen that the addition of ganglionic centres, as instruments of new functions, leaves those which were previously existing, in the discharge of their original duties.—So far as the results of experiments can be relied-on, they afford a corroboration of these views, by showing that sensory impressions can be felt, and automatic movements excited or directed, through the medium of these ganglia, after the complete removal of the Cerebrum. Thus if a Bird be thus mutilated, it maintains its equilibrium, and recovers it when it has been disturbed; if pushed, it walks; if thrown into the air, it flies. A pigeon deprived of its cerebrum has been observed to seek-out the light parts of a partially-illuminated room in which it was confined, and to avoid objects that lay in its way; and at night, when sleeping with closed eyes and its head under its wing, it raised its head and opened its eyes upon the slightest noise. It is scarcely possible to believe that these movements were merely excito-motor; since they seem obviously to indicate the guiding influence of *sensation*.

679. The results of experiments made upon the Sensory Ganglia themselves, and upon the organs from which they derive their impressions, manifest the remarkable influence of such impressions in guiding the ordinary movements of the lower animals; these being completely disturbed, and a new set of purely-automatic movements being substituted, when the ordinary relations of the organs are interfered-with.—Thus it has been ascertained by Flourens, that a vertiginous movement may be induced in pigeons, by simply blindfolding one eye; and Longet has produced the same effect, by evacuating the humours of one eye. These vertiginous movements are more decided and prolonged, when, instead of one eye being blinded, one of the optic ganglia is removed; the animal continuing to turn itself towards the injured side, as if rotating on an axis.—So, too, it was found by M. Flourens, that injury of the portion of the Auditory nerve proceeding to the 'semi-circular canals' (§ 715), would occasion still greater irregularities of movement. Section of the horizontal semi-circular canal in Pigeons, on both sides, induces a rapid jerking horizontal movement of the head, from side to side; with a tendency to turn to one side, which manifests itself whenever the animal

attempts to walk forwards. Section of a vertical canal, whether the superior or inferior, of both sides, is followed by a violent vertical movement of the head. And section of the horizontal and vertical canals, at the same time, causes horizontal and vertical movements. Section of either canal on one side only, is followed by the same effect as when the canal is divided on both sides; but this is inferior in intensity. The movements continue to be performed during several months. In Rabbits, section of the horizontal canal is followed by the same movements as those exhibited by Pigeons; and they are even more constant, though less violent. Section of the anterior vertical canal causes the animal to make continued forward 'somersets;' whilst section of the posterior vertical canal occasions continual backward 'somersets.' The movements cease when the animal is in repose; and they recommence when it begins to move, increasing in violence as its motion is more rapid. These curious results are supposed by M. Flourens to indicate, that the nerve supplying the semi-circular canals does not minister to the sense of hearing, but to the direction of the movements of the animal; but they are fully explicable, upon the supposition, that the normal function of the semi-circular canals is to indicate to the animal the *direction* of sounds (§ 715), and that its movements are partly determined by these: so that a destruction of one or other of them will produce an irregularity of movement (resulting, as it would seem, from a sort of giddiness on the part of the animal), just as when one of the eyes of a bird is covered or destroyed, as in the experiments previously cited.

680. Notwithstanding that, in Man, the high development of *Intelligence* supersedes in great degree the operations of *Instinct*, we still find that there are in ourselves certain movements, which can be distinguished as neither voluntary nor excito-motor, and which are examples of that method of operation, which seems to be the chief source of the actions of the lower Vertebrata, as of the Invertebrated classes in general. These movements are as truly 'reflex' as are the excito-motor actions of the Spinal Cord; but differ from them in this, that they are only excited by impressions of which we are conscious, that is, by sensations; and hence they are conveniently designated as *sensori-motor* or *consensual.*—As examples of this group, we may advert to the act of Vomiting, produced by various causes which act through the organs of sense; such as the sight of a loathsome object, a disagreeable smell, or a nauseous taste. The excitement of the act of Sneezing by a dazzling light, is another example of the same kind; for even if it be granted, that the act of sneezing is ordinarily excited through the spinal system alone (which is by no means certain), there can be no doubt that in this instance it cannot be brought into play without a sensation actually felt. The same may be said of the Laughter which sometimes involuntarily bursts-forth, at the provocation of some sight or sound, to which no distinct ludicrous idea or emotion can be attached; and of that resulting from the act of tickling, in which case it is most certainly occasioned by the sensation, and by that alone. The start produced by a loud and unexpected sound, and the closure of the eyes to a dazzling light, or on the sudden approach of a body that might injure them (which has been observed to take place in certain cases of paralysis, in which the eyelids could not be *voluntarily* closed), are additional examples of the same kind. It is in certain morbid states, however, that the direct influence of Sensations in occasioning and

governing movements, in a manner not to be accounted-for either by excito-motor or by voluntary action, is most remarkably manifested. Thus in cases of excessive irritation of the retina, which renders the eye most painfully sensitive to even a feeble amount of light,—the state designated as *photophobia*,—the eyelids are drawn-together spasmodically, with such force as to resist very powerful efforts to open them; and if they be forcibly drawn-apart, the pupil is frequently rolled beneath the upper lid, much further than it could be carried by a voluntary effort. And in painful affections of the walls of the chest, we may observe the usual movements of the ribs to be very much abridged; the dependence of this abridgment upon the painful sensation which they occasion, being most evident in those instances in which the affection is confined to one side,—for there is then a marked curtailment in *its* movements, whilst those of the other side may take-place as usual; a difference which can scarcely be 'excito-motor,' and which the Will cannot imitate. Again, in some Convulsive disorders, we may notice that the paroxysms are excited by causes, which act through the organs of special sense; thus in Hydrophobia, we observe the immediate influence of the sight or the sound of liquids, and of the slightest currents of air; and in many Hysteric subjects, the sight of a paroxysm in another individual is the most certain means of its induction in themselves.

681. When we contrast the actions of Man and of the higher Vertebrata, with those of the lower, we cannot but perceive that we gradually lose the indications of *Intelligence* and *Will*, as the sources of the movements of the animal; whilst we see a corresponding predominance of those, which are commonly denominated *Instinctive*, and which are performed (as it would appear) in immediate respondence to certain sensations, without any *intentional* adaptation of means to ends on the part of the individual; although such adaptiveness doubtless exists in the actions themselves, being a consequence of the original constitution of the nervous system of each animal performing them. It cannot be doubted by any person who has attentively studied the characters of the lower animals, that many of them possess psychical endowments, corresponding with those which we term the Intellectual powers and Moral feelings in Man; but in proportion as these are undeveloped, in that proportion is the animal under the dominion of those instinctive impulses, which, so far as its own consciousness is concerned, may be designated as blind and aimless, but which are ordained by the Creator for its protection from danger, and for the supply of its natural wants. The same may be said of the Human infant, or of the Idiot, in whom the reasoning powers are undeveloped. Instinctive actions may in general be distinguished from those which are the result of voluntary power guided by reason, chiefly by the two following characters:—1. Although, in many cases, experience is required to give the Will command over the muscles concerned in its operations, no experience or education is required, in order that the different actions, which result from an Instinctive impulse, may follow one another with unerring precision.—2. These actions are always performed by the same species of animal, nearly if not exactly, in the same manner; presenting no such variation in the means adapted to the object in view, and admitting of no such improvement in the progress of life, or in the succession of ages, as we observe in the habits of individual men, or in the manners and customs of nations, that are adapted to the attainment of

any particular ends, by those voluntary efforts which are guided by reason. —3. The fact, too, that these Instinctive actions are often seen to be performed under circumstances rendering them nugatory, as reason informs us, for the ends which they are to accomplish (as when the domesticated Beaver builds a dam across its apartment, or when the Bee tries to produce a queen from drone-larvæ), is an additional proof, that such actions are prompted, like the excito-motor and consensual movements we have been just inquiring-into, by an impulse which immediately results from a particular impression or sensation, and not by anticipation of the effect which the action will produce.*

682. So far as can be determined by the foregoing tests, we find the comparative predominance of the *Instinctive* actions and the *Intelligent*, to be in close accordance with the relative development of the *Cranio-Spinal Axis* and the *Cerebrum*. And since some of the actions which have been designated as Instinctive, such as that of sucking in the Infant (§ 677), have been shown to be purely 'excito-motor,' not even involving consciousness, we seem fully justified in the conclusion, that the Instinctive actions of animals are truly 'automatic' in their character, and that they are performed by the instrumentality of the Cranio-Spinal Axis in Vertebrata, and of the Ganglia which correspond to them in Invertebrated animals. We must look for their origin, then, in impressions made upon the afferent nerves, either by external objects, or by changes taking place in the internal organisation (such, for example, as the periodic development of the sexual organs); which impressions will excite respondent or 'reflex' movements, either through the ganglia of 'sensori-motor' or those of 'excito-motor' action, according as they are, or are not, of a nature to require the *consciousness* of the animal to be called-forth, as a link in the chain of their operation upon the muscular system.†

683. But we may trace the agency of the Sensory-Ganglia, in Man

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* See Prof. Alison's Article 'Instinct,' in "Cyclop. of Anat. and Phys.," Vol. III.

† The highest development of the purely Instinctive tendencies, with the least interference of Intelligence, is to be found in the class of Insects; and above all in the order *Hymenoptera*, and in that of *Neuroptera*, which is nearly allied to it. It is, of course, impossible to draw the line between the two sources of action, with complete precision; but we observe, in the habits of Bees and other social Insects, every indication of the limitation of the power of choice, and of the domination of instinctive propensities called into action by sensations. Thus, although Bees display the greatest art in the construction of their habitations, and execute a variety of curious contrivances, beautifully adapted to variations in their circumstances, the constancy with which individuals and communities will act alike under the same conditions, appears to preclude the idea of their possessing any inherent power of spontaneously departing from the line of action, to which they are tied-down by the constitution of their Nervous system. We do not find one individual or one community clever, and another stupid; nor do we ever witness a disagreement, or any appearance of indecision, as to the course of action to be pursued by the several members of any republic. The actions of all tend to one common end, simply because they are performed in respondence to impulses, which all alike share. For a Bee to be destitute of its peculiar tendency to build at certain angles, would be as remarkable as for a Human being to be destitute of the desire to eat, when his system should require food.—Still the Author would by no means maintain that there are, even among Bees, *no* manifestations of Intelligence; for a careful study of their habits shows that they do profit by experience, in a manner that shows a certain amount of educability. And this faculty may not improbably be connected with the presence of a rudimentary Cerebrum, which is capable of being distinguished from the Sensorial centres that constitute the principal part of their Cephalic Ganglia. See the Memoirs of M. Dujardin 'Sur le Cerveau des Insectes,' and 'Sur les Actes qui, chez les Abeilles, peuvent etre rapportés à l'Intelligence,' in "Ann. des Sci. Nat.," 3^e Sér., Zool., Tom. XIV., XVIII.

and the higher Vertebrata, not merely in their direct and independent operation on the Muscular system, but also in the manner in which they participate in all Voluntary actions. There can be no doubt that, in every exertion of the *Will* upon the muscular system, we are guided by the sensations communicated through the afferent nerves, which indicate to the Sensorium the state of the muscle. Many interesting cases are on record, which show the necessity of this 'Muscular Sense,' for determining voluntary contraction of the muscle. Thus, Sir C. Bell (who first prominently directed attention to this class of facts, under the designation of the *Nervous Circle*), mentions an instance of a woman, who was deprived of it in her arms, without losing the motor power; and who stated, that she could not sustain anything in her hands (not even her child), by the strongest effort of her Will, unless she kept her eyes constantly fixed upon it; the muscles losing their power, and the hands dropping the object, as soon as the eyes were withdrawn from it. Here the employment of the *visual* sense supplied the deficiency of the *muscular*; but instead of being inseparably connected, as the latter is in the state of health, with the action of the muscle, the former could be only brought to bear upon it by an effort of the will; and the sustaining power was therefore dependent, not upon the immediate influence of the will upon the muscle, but upon the voluntary direction of the sight towards the object to be supported.—Again, in the production of vocal sounds, the nice adjustment of the muscles of the larynx, which is requisite to produce determinate tones (§§ 734-736), can only be learned in the first instance under the guidance of the sensation of the sounds produced, and can only be effected by an act of the Will, in obedience to a mental conception (a sort of inward sensation) of the tone to be uttered; which conception cannot be formed, unless the sense of hearing has previously brought similar tones to the mind. Hence it is, that persons who are born *deaf*, are also *dumb*. They may have no malformation of the organs of speech; but they are incapable of uttering distinct vocal sounds or musical tones, because they have not the guiding conception, or recalled sensation, of the nature of these. By long training, and by efforts directed by the muscular sense of the larynx itself, some persons thus circumstanced have acquired the power of speech; but the want of a sufficiently definite control over the vocal muscles, is always very evident in their use of the organ.—The conjoint movement of the two eyes, which concur to direct their axes towards the same object, are among the most interesting of these actions, in which Volition and Consensual action are alike concerned; and they afford an excellent illustration of the necessity for guiding sensations, to determine the actions of muscles. The sensations, however, are not so much those of the muscles themselves, as those received through the visual organ; but the former appear capable of continuing to guide the harmonious movements of the eyeballs, when the sense of sight has been lost. It is a striking peculiarity of these movements, that, in the majority of them, two muscles or combinations of muscles of opposite action are in operation at once; thus, when the eyes are made to rotate in a horizontal plane, the internal rectus of one side acts with the external rectus of the other.—In most other cases, there is a difficulty in performing two opposite movements on the two sides, at the same time. Thus although, if we move the right hand as if winding on a reel, and *afterwards* make the left hand revolve in a contrary direction, no difficulty is experienced; yet if we attempt to move the two *at the same time* in contrary directions, we shall find it almost impossible.

684. It is not difficult to account, on the foregoing principles, for the fact which has been a source of great perplexity to Metaphysicians and Physiologists,—that movements which were at first performed Voluntarily, and which even required a distinct effort of the Will for each, may become, by habitual repetition, so far independent of the will, that they are performed when the whole attention of the mind is bestowed upon some other train of action. Thus we all know that, in walking along an accustomed road, we frequently occupy our minds with some perfectly continuous chain of reasoning; and yet our limbs continue to move under us with regularity, until we are surprised by finding ourselves at the place of our destination, or perhaps at some other, which we had not intended to visit, but to which habit has conducted us. Or we may read aloud for a long time, without having in the least degree comprehended the meaning of the words we have uttered; our attention having been closely engaged by some engrossing thoughts or feelings within. Or a musician may play a well-known piece of music, whilst carrying-on an animated conversation.—Some Metaphysicians have explained these facts by supposing, that (as the mind cannot *will* two different things at the same time) the Volition is in a sort of vibratory condition between the two sets of actions, now prompting one and now the other. But it would seem much more conformable to the analogy afforded by other physiological phenomena, to regard these, with Hartley, as 'secondarily automatic;' that is, as taking the place, in Man, of those actions which are primarily and purely automatic in many of the lower animals, in virtue of the tendency which may be noticed in the whole of his organisation, but which is pre-eminently remarkable in his Nervous System, to develope itself in the mode in which it is habitually exercised. We shall see that, even when most purely Voluntary, these actions are performed by the instrumentality of the automatic apparatus (§ 693); and under the influence of habit, the movements become gradually linked-on to the sensations which at first guided them, in such a manner that the latter at last come to be themselves adequate excitors of the movement, when the series has been once commenced by an exertion of the will. It has been thought by some to be a sufficient proof of the voluntary nature of these movements, that we can check them at any time by an effort of the will; but this we do, only when the attention has been recalled to them, so that the Cerebrum, liberated as it were from its previous self-occupation, resumes its usual play upon the automatic centres. In the performance of such habitual actions, it would seem as if, the first *start* having been given by the will, the sensation involved in each movement becomes the stimulus to the next, and so on, until the habitual series is concluded, or the attention is called-back to them.—This view is confirmed by the fact, that in cases of severe injury of the Brain, in which Intelligence and Will seem completely in abeyance, actions that have become habitual may often be excited.

685. That the *Cerebellum* is in some way connected with the powers of *motion*, might be inferred from its connection with the antero-lateral

columns of the Spinal Cord, as well as with the posterior; and the comparative size of the organ, in different orders of Vertebrated animals, gives us some indication of what the nature of its function may be. For we find its degree of development to correspond pretty closely with the variety and complexity of the Muscular movements, which are habitually executed by the species; the organ being the largest in those animals, which require the *combined* effort of a great variety of muscles to maintain their usual position, or to execute their ordinary movements; whilst it is the smallest in those, which require no muscular exertion for the one purpose, and little combination of different actions for the other. Thus in animals that habitually rest and move upon four legs, which is the case with most Reptiles, there is comparatively little occasion for any organ to combine and harmonize the actions of their several muscles; and in these, the Cerebellum is usually small. But among the more active predaceous Fishes (as the Shark), Birds of the most powerful and varied flight (as the Swallow), and such Mammals as can maintain the erect position, and can use their extremities for other purposes than support and motion, we find the Cerebellum of much greater size, relatively to the remainder of the Encephalon. There is a marked advance in this respect, as we ascend through the series of Quadrumanous Animals, from the Baboons, which usually walk on all-fours, to the semi-erect Apes, which often stand and move on their hind-legs only. The greatest development of the Cerebellum is found in Man, who surpasses all other animals in the number and variety of the combinations of muscular movement which his ordinary actions involve, as well as of those which he is capable, by practice, of learning to execute.—From experiments upon all classes of Vertebrated animals, it has been found that, when the Cerebellum is removed, the power of walking, springing, flying, standing, or maintaining the equilibrium of the body, is destroyed. It does not seem that the animal has in any degree lost the *voluntary* power over its individual muscles; but it cannot *combine* their actions for any general movements of the body. The *reflex* movements, such as those of respiration, remain unimpaired. When an animal thus mutilated is laid on its back, it cannot recover its former posture; but it moves its limbs, or flutters its wings, and evidently is not in a state of stupor. When placed in the erect position, it staggers and falls like a drunken man; not, however, without making efforts to maintain its balance. Phrenologists, who attribute a different function to the Cerebellum, have attempted to put aside these results, on the ground that the severity of the operation is alone sufficient to produce them; but, as we have already seen (§ 678), many animals may be subjected to a much more severe operation, the removal of the Cerebral hemispheres, without the loss of the power of combining and harmonizing the muscular actions, provided the Cerebellum be left uninjured.—Thus, then, the idea of the functions of the Cerebellum, which we derive from Comparative Anatomy, seems fully borne-out by the results of experiment; and it is also consistent with the conclusions to which observation of Pathological phenomena seems to lead. Some of these phenomena, however, appear to indicate that either the median lobe of the Cerebellum, or some collection of ganglionic matter in its vicinity, is the centre of *sexual* sensibility, which seems to be distinct from 'common' or 'tactile' sensibility.

686. It appears to be through the instrumentality of the *Cerebrum* or *Hemispheric Ganglia*, that the sensations awakened in the Sensorium give rise to *Ideas;* which then become the material (so to speak) of all the higher psychical operations. It is not alone, however, by the exercise of the Reasoning faculties, leading to Volitional determinations, that mental states react upon the motor apparatus: for we find that not only does *emotional* excitement give rise to movements, which are as involuntary as the automatic, and which the reason and will may in vain endeavour to keep in check; but that muscular movements may also proceed directly from *ideas* which have possession of the mind, and this especially when the controlling power of the Will is weakened or withdrawn, as happens in Man, in the states of Somnambulism, Reverie, &c. Such movements may be considered to depend on a 'reflex action' of the Cerebrum, just as the 'excito-motor' and 'consensual' classes of movements are dependent on the 'reflex action' of the Spinal Cord and Sensory Ganglia respectively. And there is strong ground for the belief, that much of what is attributed to 'Intelligence' among the lower animals, and in human childhood, must be set down to this automatic operation of the instrumental organ of Thought.

687. It has been supposed by some, that the *Emotional* movements of Man and the higher animals, might be ranked in the same category with the *Instinctive* actions of the lower; and that the *Desires* of the former are comparable to the *Instinctive Propensities* of the latter. But this comparison is erroneous; for such 'propensities,' as already shown, are nothing else than *tendencies to perform* given movements in respondence to particular sensations, without any idea of the purpose of the movement, or of the object which has excited it; whereas an 'emotion' involves an idea of the object which has excited it, and a 'desire' involves a conception of the object to be attained. The *Imitative* tendency will afford a good example of the difference between a 'propensity' and a 'desire.' The former is manifested in such imitative actions as are purely 'consensual,' the sensation in each case exciting the movement automatically; as when we yawn involuntarily, from seeing or hearing the action performed by another; or as when infants learn to perform many of the movements which they witness in adults. But in other instances, imitative actions are the result of a *desire* to perform them, which involves a distinct idea of the object; and are at the same time a source of pleasure to the performer, which is the spring of the desire. Thus we find the two sources of action to be so distinct, that the tendency to involuntary or automatic imitation may be very strong in an individual, who is utterly unable to mimic or imitate voluntarily, and who has no conscious inclination to do so; whilst on the other hand, the power of volitional imitation may co-exist to a remarkable extent, with an absence of all tendency to 'catch' peculiar gestures, pronunciations, &c., involuntarily.

688. Now when the *Emotions* and *Moral Feelings* are analyzed, we find them to be complex in their nature; being made-up by the association of *ideas,* which are Cerebral in their seat, with the simple *feelings* of pleasure and pain, and other more special forms of *Emotional sensibility,* which are probably localized in the Sensorium. Thus, Benevolence may be defined to be the pleasurable idea of the happiness of others; the whole class of Selfish emotions, on the other hand, is nothing else than

the pleasurable contemplation of objects of supposed value to self; Combativeness, again, is the pleasurable idea of antagonism to others; Veneration, the pleasurable contemplation of rank or perfections superior to our own; Hope, the pleasurable anticipation of future enjoyment; Cautiousness, a combination of the painful contemplation of future evil, with the pleasurable idea of the precautions taken to prevent it.—Now when emotions are excited by external sensations, these emotions may act downwards through the automatic system, producing movements which may be in direct antagonism to the Will. Thus we may see or hear something ludicrous, which involuntarily provokes laughter, although we may have the strongest possible motives for desiring to restrain it. The essential distinctness between Emotional and Volitional actions is further indicated by this; that cases of paralysis not unfrequently occur (especially in the facial nerve, through which the muscles of 'expression' are for the most part excited to action), in which the muscles are obedient to an emotional impulse, though the will exerts no power over them; whilst in other instances, the will may exert its due influence, and yet the emotional state cannot manifest itself. There are, moreover, several disordered states of the nervous system (such as Chorea and Hysteria), in which irregular or convulsive movements, totally unrestrainable by the will, are directly consequent upon emotional excitement.—The purely Emotional movements are not always directly excited, however, by *external* sensations; for they may result from the operations of the Mind itself. Thus, involuntary laughter may result from a ludicrous *idea*, called-up by some train of association, and having no obvious connection with the sensation which first set this process in operation; and the various movements of the face and person, by which Actors endeavour to express strong Emotions, are most effectual in conveying their meaning, when they result from the actual working of the emotions in the mind of the performer, who has, by an effort of the will, identified himself (so to speak) with the character he personates. A still more remarkable case is that, in which paroxysms of Hysterical convulsion, in themselves beyond the power of the Will to excite or to control, are brought-on by a voluntary effort; which seems to act by 'getting-up,' so to speak, the state of feeling which is the immediate cause of the disordered movements. In all these instances, and others of like nature, it would seem as if the agency of the Cerebrum produced the same condition in the Sensory ganglia and their motor fibres, as that which is more directly excited by sensations received through their own afferent nerves.—The Emotions are concerned in Man, however, in many actions which are in themselves strictly voluntary. Unless they be so strongly excited as to get the better of the Will, they do not operate downwards upon the motor system, but upwards upon the Cerebral; supplying the chief *motives* by which the voluntary determinations are guided (§ 691).

689. Very distinct proof has been afforded by recent enquiries, that there are acts of mind upon the body, which are neither Volitional nor Emotional, but originate in the intense excitement of *Ideas*, which have, for the time, full possession of the consciousness, and express themselves in muscular movements. Such ideas may have been either directly excited by sensations, or secondarily developed by reasoning processes; they may either remain obstinately fixed in the mind, or they

may be capable of being displaced by others newly excited through internal or external suggestion. In any case, nothing more is required than that they should possess a certain degree of intensity, and that the Will should exert no antagonizing influence, for them to operate directly upon the motor nerves; and this they may do, when the Will is in a state of abeyance (as in the states of Dreaming, Somnambulism, or Abstraction), or when it simply exerts a permissive influence (as in a large proportion of our ordinary actions, which may be traced to the direct influence of the ideas that occupy our minds at the time), or even, provided that the ideas attain the force of 'convictions,' in opposition to the Will (as we see in 'biologized' subjects who are made to believe that they *must* do *this*, or *cannot* do *that*, however much they may strive to act in opposition to the assurance). It is in those peculiar states of the Human Mind, in which, the power of the Will over the current of Thought being entirely suspended, any Idea that may for the time be present to the consciousness acquires a complete 'dominance' (however much it may be opposed to the ordinary experience and common-sense of the individual), that we have the most remarkable exemplification of this kind of action, which may be designated as *ideo-motor*. But that which is abnormal in Man, seems to be the normal condition of the Animals which most nearly approach him; for, so far as we can judge of their psychical endowments from their actions, these seem to operate 'automatically;' their ideas expressing themselves directly in action, without being subject to any volitional regulation, just as do those of a Somnambule; and the course of their thoughts being entirely governed by external impressions, or by the remembrance (automatically excited) of past ideas or emotions.

690. In general, however, the operation of Ideas is not directly to call forth movements, but to *suggest* other ideas in a more or less orderly sequence, constituting what is known as a *train of thought*. The nature of this sequence will depend in part upon the original constitution of the species and of the individual, and partly (in Man especially) upon the habits of thought which may have been previously acquired: and the capacity for each particular mode of mental activity, which may thus be either 'original' or 'acquired,' is designated a *mental faculty;* whilst the sum of all the faculties, together with those Emotional tendencies which in great degree determine the mode and degree of their exercise, constitutes the *character*.—Among these faculties, of which the *Cerebrum* seems to be the instrument, the following may be specified as of fundamental importance. That of *Memory*, which is one of those first awakened in the opening mind of the Infant, and one of which we find traces in animals that seem to be otherwise governed by pure Instinct, is obviously the first step towards the exercise of the Reasoning powers; since no *experience* can be obtained without it; and the foundation of all intelligent adaptation of means to ends, lies in the application of the knowledge which has been acquired and stored-up in the mind. There is strong reason to believe that no impression of this kind, once made upon the Cerebrum, is ever entirely lost, except through disease or accident, which will frequently destroy the memory altogether, or will annihilate the recollection of some particular class of objects or of words. All memory, however, seems to depend upon the principle of Suggestion; one idea being linked with another, or with a particular sensation, in such a manner as to be called-

up by its recurrence; and a period of many years frequently intervenes, without that combination of circumstances presenting itself, which is requisite to arouse the dormant impression of some early event. Sometimes this combination occurs in dreaming, delirium, or insanity; and ideas are recalled, of which the mind, in a state of healthy activity, has no remembrance.—It is upon the ideas directly aroused in the mind by Sensorial changes, or brought back to the consciousness by *Recollection*, or evolved by the process of *Reflection* (in which the mind perceives its own operations, and traces relations amongst its objects of thought), or generated by the *Imagination* (which really acts, however, rather by combining into new forms than by creating altogether *de novo*), that all acts of *Reasoning* are based. These consist, for the most part, in the aggregation and collocation of ideas, the decomposition of complex ideas into more simple ones, and the combination of simple ideas into general expressions; in which are exercised the faculty of *Comparison*, by which the relations and connections of ideas are perceived,—that of *Abstraction*, by which the attention is fixed on any particular qualities of the object of our thought, and isolated from the rest,—and that of *Generalisation*, by which we grasp in our minds some definite notions in regard to the general relations of those objects. Notwithstanding that such processes are distinguished by their *psychical* nature from those already considered, they must be regarded as in themselves essentially 'automatic,' and as constituting the manifestation of the 'reflex' activity of the Cerebrum. There is, it is true, far less of uniformity among them, than we observe in the reflex actions of other parts of the Nervous Centres; but this want of constancy seems attributable in part to diversities in the *original* constitution of the organ in different individuals, and in part to diversities in its *acquired* constitution, arising out of the mode in which they have been habitually exercised, as in the case of the 'secondarily-automatic' actions of the Cranio-Spinal axis (§ 684). These Mental operations, however, are peculiarly amenable to the control of the Will; by which the attention is directed to any one object of thought, to the exclusion of others, and the whole power of the Intellect thus concentrated upon it (§ 692).

691. The purely Intellectual processes are those chiefly concerned in the simple acquirement of *Knowledge;* with which class of operations, the Emotional part of our nature has very little participation. But in those modes of exercise of our Reasoning powers, which are chiefly concerned in the determination of our *conduct*, the Emotions, &c., are largely concerned. They chiefly (if not solely) act upon the reasoning powers, by modifying the form in which the ideas are presented to the mind; whether these ideas are directly excited by external Sensations, or whether they are called-up by an act of the Memory, or result from the exercise of the Imagination. For as they essentially consist of pleasurable or painful feelings, connected with certain classes of ideas, the former produce a *desire* of the objects to which they relate, the latter a *repugnance* to them. They thus have a most important influence upon the *Judgment*, which is formed by the comparison of certain kinds of ideas; and they may consequently modify the Volitional determination, or act of the Will, which is consequent upon this, and which may either be directed towards the further operations of the mind itself, or may exert an immediate influence on the bodily frame, by the agency of the Nervous System.

In either case, it is the characteristic distinction of a Volitional operation, that *means are intentionally*, and by a conscious effort, *adapted to ends*, in accordance with the belief of the mind as to their mutual relations. Upon the correctness of that decision, will depend the power of the action to accomplish what the mind had in view.

692. The power of the *Will*, when fully developed in Man, is especially exerted in controlling and directing the 'automatic' activity of the Cerebrum; regulating the course and succession of Ideas, as well as the degree of Emotional excitement, by its power of fixing the attention on any object of thought which it may determine to pursue, and of withdrawing it from whatever it may desire to keep out of the mental view. This seems to be the most distinctive attribute of the Human mind in its highest phase of evolution; and it is this which gives to each individual that freedom of action, which every one is conscious to himself that he is capable of exerting. For, notwithstanding the evidences of rationality which many of the lower animals present, and the manifestations which they display of emotions that are similar to our own, there is no ground to believe that they have any of that controlling power over the psychical operations, which *we* enjoy; on the contrary, all observation leads to the conclusion, that they are under the complete domination of the ideas and emotions by which they are for the time possessed, and have no power either of repressing these by a forcible effort of the Will, or of turning the attention, by a like determinate effort, into another channel. In the early stages of the development of the Human mind, a precisely-similar state may be observed; the course of thought in the young child being entirely governed by 'suggestion,' and his actions being the expression of the idea that may happen at the time to be 'dominant' in his mind. And there are adults who have acquired so little of this power of self-control, that they can scarcely be said to be truly-Voluntary agents; some being so much accustomed, in consequence of the weakness of their Will, to act directly upon the idea or emotion that may gain a momentary prominence in their minds, and being thus characterized by an infirmity of purpose which may amount to actual imbecility; whilst others allow certain dominant ideas or habitual feelings to gain such a mastery over them, as to exercise that determining power which the Will alone ought to exert, thus approaching the 'mono-maniacal' form of Insanity. On Man's power of self-direction, all the highest development, alike of his Intellectual powers and of his Moral nature, essentially depends; and it is especially by this *progressive* element in his psychical constitution, that it is distinguished from that of the lower animals.—The power of the Will to direct the course of thought, however, is not unlimited; for it can only utilize the capacities which each individual possesses, by selecting from those ideas and feelings which may present themselves to his consciousness, such as he desires to retain and employ; thus cultivating and strengthening his Intellectual powers, expanding and elevating his Imagination, and training and disciplining his Moral nature. The Will has no power of directly bringing before the mind that which is not already present to it; and thus it cannot introduce new elements into any Man's psychical nature, although it enables him to turn to the most advantageous account whatever he may possess. Hence arises that limitation of his capacity for progress, which is involved in the very nature of his present existence.

693. Although Physiologists have been accustomed to regard the *Will* as *directly determining* all those muscular movements which are usually distinguished as Voluntary, yet a careful analysis of the process fully bears-out the inferences which might be erected upon the considerations already advanced,—that the influence of the Will is *not* directly conveyed to the muscles by fibres beginning in the Cerebral convolutions and proceeding to the muscles, but that it is exerted through the Cranio-Spinal axis. For it has been shown that this collection of centres (the Sensory Ganglia, Medulla Oblongata, and Spinal Cord) receives all the sensory nerves, and gives origin to all the motor; and that the fibres which pass between the cerebral convolutions and the sensory ganglia, probably serve merely to bring these organs into mutual relation, and are not continuous with those of any nerves, either sensory or motor.—Now every one who has attentively considered the nature of what we are accustomed to call *voluntary* action, has been struck with the fact, that the Will simply determines the *result*, not the special movements by which that result is brought-about. If it were otherwise, we should be dependent upon our anatomical knowledge, for our power of performing even the simplest movements of the body. Again, there are very few cases in which we can single-out any individual muscle, and put it in action independently of others; and the cases in which we *can* do so, are those in which a single muscle is concerned in producing the result,—as in the elevation of the eyelid; and we then really single-out the muscle, by 'willing' the result. Thus, then, however startling the position may at first appear, we have a right to affirm that the Will cannot exert any direct or immediate power over the muscles; but that its determinations are carried into effect through an intermediate mechanism, which, without any further guidance on our own parts, selects and combines the particular muscles whose contractions are requisite to produce the desired movement. We have seen that the Sensorium (or collection of sensory ganglia) *plays*, so to speak, upon the Cerebrum; sending to it sensational changes, whereby its peculiar activity as an instrument of purely mental operations is called forth; and, in return, the Cerebrum appears to *play* downwards upon the motor portion of the automatic apparatus, sending to it volitional impulses, which excite its motorial activity. And, hence, it follows that *all* the movements which are performed by the instrumentality of the cerebro-spinal nervous system, are in themselves *automatic;* and that the peculiarity in their character,—whether Excito-motor, Consensual, Ideational, Emotional, or Voluntary,—is due to the speciality of the source and seat of the impulses which respectively originate them.

694. The nerves of the *Sympathetic* System,—in which tubular fibres derived from the Cerebro-spinal system are combined in various proportions with those 'grey' or 'organic' fibres which have their centres in the proper Sympathetic ganglia,—possess a certain degree of power of exciting Muscular contractions, in the various parts to which they are distributed. Thus by irritating them, immediately after the death of an animal, contractions may be excited in any part of the alimentary canal, from the pharynx to the rectum, according to the trunks which are irritated; in the heart, after its ordinary movements have ceased; in the aorta, vena cava, and thoracic duct; in the ductus choledochus,

uterus, fallopian tubes, vas deferens, and vesiculæ seminales. But the very same contractions may be excited, by irritating the roots of the Spinal nerves, from which the Sympathetic trunks receive their white fibres; and there is, consequently, strong reason to believe, that the *motor* power of the latter is entirely dependent upon the Cerebro-spinal system. Whatever *sensory* endowments the Sympathetic trunks possess, are probably to be referred to the same connection. In the ordinary condition of the body, these are not manifested. The parts exclusively supplied by Sympathetic trunks do not appear to be in the least degree sensible; and no sign of pain is given, when the Sympathetic trunks themselves are irritated. But in certain diseased conditions of those organs, violent pains are felt in them; and these pains can only be produced, through the medium of fibres communicating with the Sensorium through the spinal nerves.—It is difficult to speak with any precision, as to the functions of the Sympathetic system. There is much reason to believe, however, that it constitutes the channel, through which the passions and emotions of the mind affect the Organic functions; and this especially through its power of regulating the calibre of the arteries. We have examples of the influence of these states upon the Circulation, in the palpitation of the heart which is produced by an agitated state of feeling; in the Syncope, or suspension of the heart's action, which sometimes comes-on from a sudden shock; in the acts of Blushing and turning pale, which consist in the dilatation or contraction of the small arteries; in the sudden increase of the salivary, lachrymal, and mammary Secretions, under the influence of particular states of mind, which increase is probably due to the temporary dilatation of the arteries that supply the glands, as in the act of blushing; and in many other phenomena. It is probable that the Sympathetic system not only thus brings the Organic functions into relation with the Animal: but that it also tends to harmonize the former with each other, so as to bring the various acts of Secretion, Nutrition, &c., into mutual conformity. Of the distinctive function of the 'grey' or 'organic' fibres and of their ganglionic centres, constituting the proper *visceral* system, we have no certain knowledge; but they not improbably may have some direct influence upon the chemical processes which are involved in such changes, and may thus affect the *quality* of the secretions; whilst the office of the tubular fibres may be rather to regulate the diameter of the blood-vessels supplying the glands, and thus to determine the *quantity* of their products.

3. *General Summary.*

695. A retrospective view of the ground over which we have now passed, will lead us to some interesting conclusions.

I. It has been shown that the movements occasionally exhibited in the Vegetable kingdom, do not imply the existence, in its members, of Consciousness or of a guiding Will; being merely dependent upon that property of *contractility* upon the application of a stimulus, which may be regarded as due to the peculiar manner in which the elements of the contractile tissues are combined and arranged. Hence Vegetables may be considered as peculiarly, though not exclusively, constituting the *Kingdom of Organic Life.*

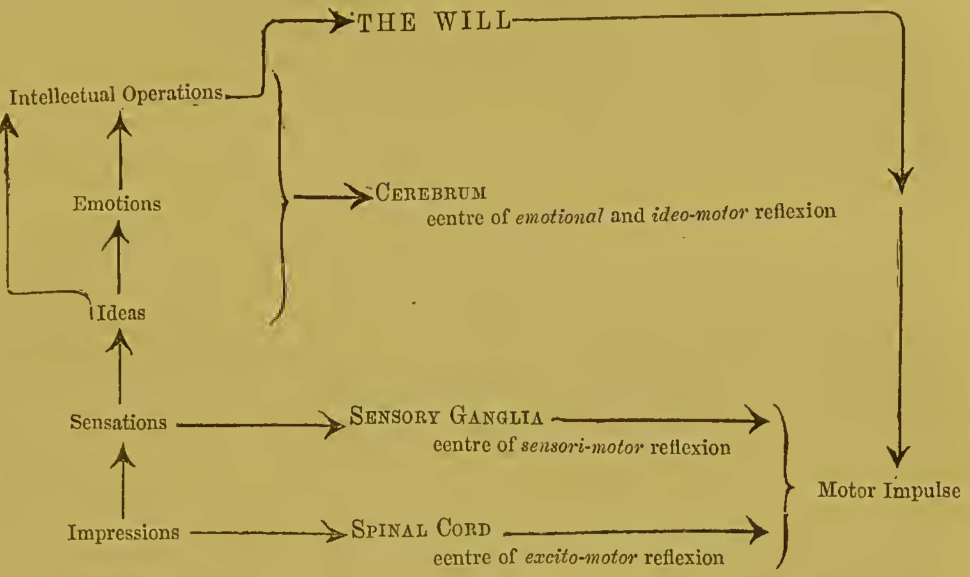
II. In immediate connection with the lowest of the Vegetable kingdom, are the lowest of the Animal tribes, the *Protozoa* and lower *Radiata*. Here we see indications of the same simple contractility which Plants enjoy; but this has a more important relation to the well-being of the individual, and forms a more prominent part of its vital actions. The movements which they exhibit, are not, any more than the like movements presented by Plants, to be in themselves regarded as manifestations of consciousness; and we have no other evidence of their possession of sensibility. Still, although no distinct Nervous System can be detected in them, there is an analogical probability that some *feeling,* however obscure and indefinite, is excited by impressions made upon them, probably resembling that which we ourselves derive from states of the digestive apparatus.

III. In addition to the movements proceeding from the direct excitement of contractile tissues, we witness others, in the higher *Radiata,* and in the lower *Articulata* and *Mollusca,* which are consequent upon impressions made on distant parts and transmitted through the nervous system; and some, even, which seem to be performed under the guidance of sensation; although none which clearly evince intelligence and design on the part of the animals themselves. Proceeding still further, we observe these 'instinctive' movements becoming more complex in their character, and more refined and special in their objects; until we arrive at the class of *Insects,* which seem to possess the highest development of the *Instinctive* faculties, of any known animals. But we do not find *Intelligence* by any means increasing in the same ratio. On the contrary, it remains very low; and its power of modifying the dictates of Instinct, when these happen (from particular causes) to be erroneous, is very slight. If we further inquire, in what *orders* of Insects this power is most strikingly manifested, we shall have little hesitation in fixing upon the *Hymenoptera* and *Neuroptera;* which include the Bee, Wasp, Ant, White-Ant, and other social Insects.—Now it is not a little remarkable, that Insects should, of all classes of Animals, be most distinguished for *locomotive* power (as compared with their size); and that, of all Insects, the Hymenoptera and Neuroptera possess this power in the highest degree. It is evident that the higher kinds of instinctive actions, including the peculiar endowments of the nervous and muscular systems just referred-to, have for their object the maintenance of *animal* life, as distinguished on the one hand from the mere *organic* life of Vegetables, and from the *mental* or *psychical* life of higher beings, on the other. Hence we should regard Insects, and especially the Hymenoptera and Neuroptera, as typical of the *Kingdom of Animal Life.* In this, we find the movements which are produced by the direct contractility of the tissues stimulated, bearing a smaller and still smaller proportion to the whole; and at last restricted merely to the parts immediately concerned in the maintenance of the organic functions, with which they always remain associated (§ 628).

IV. Ascending from the Articulated through the *Vertebrated* series, we observe a gradually-increasing development of the reasoning powers or Intelligence; and a gradual fading-away of the Instincts, which become subordinate to the higher psychical faculties. A comparison between the habits of Birds and those of Insects, will put this in a striking light.

Several points of structural and physiological correspondence exist between these two classes, indicating that they hold a corresponding rank in their respective sub-kingdoms. But whilst nearly all the actions of Insects appear to be under the guidance of pure unvarying instinct, those of Birds, whilst evidently prompted by similar impulses, are yet capable of great modification in each individual (according to the peculiar circumstances in which it may happen to be placed) by the influence of its reasoning faculties. Yet even in animals which possess a certain capability of determinately adapting means to ends, by the operation of a real Intelligence, and which present, moreover, some approach to the *moral* nature of Man, the psychical nature still wants that completeness which shall make them truly independent agents; for they do not seem to possess the power of determining their course of thought and of action by an effort of the Will, which is the characteristic attribute of Man, but appear to be entirely under the domination of whatever ideas or passions may for the time possess their minds.

v. When we come, however, to Man, we find the pure Instincts brought under such subordination to the higher Psychical nature, and this placed so completely under the control of the Will, that it is only when the latter is still dormant or undeveloped, as is the case in infancy or idiocy, or when the balance is destroyed by disease, as in insanity, that the unrestrained operation of the automatic tendencies is witnessed. It is easy to perceive the final cause for this change. If the organisation of the Human system had been adapted to perform all the actions necessary for the continued maintenance of his existence, with the same certainty and freedom from voluntary effort as we perceive where pure instinct is the governing principle,—and if all his sensations had given rise to intuitive perceptions, instead of those perceptions being acquired by the exercise of his mind,—it is evident that external circumstances would have created no stimulus to the improvement of his intellectual powers, and that the strength of his instinctive propensities would have diminished the freedom of his moral agency. Although, therefore, to all the actions *immediately* necessary for the maintenance of his own existence, and for the continuance of his race, a powerful instinct strongly impels him, these propensities could not be gratified, if the means were not provided by the exercise of those mental powers, which he enjoys in a degree far exceeding those of any other terrestrial being.—Hence we should be led to regard his place in the Animal Kingdom, as being not at its head or in its centre, but at the extreme most remote from its point of contact with the kingdom of Organic life; in fact, at the point at which we may believe it to touch another Kingdom, that of *pure Intelligence.* Such a view tends to show the true nobility of Man's rational and moral nature; and the mode in which he may most effectually fulfil the ends for which his Creator designed him. He may learn from it the evil of yielding to those merely animal propensities, those "fleshly lusts which war against the soul," that are characteristic of beings so far below him in the scale of existence; as well as the dignity of those pursuits which exercise the intellect, and which expand and strengthen those lofty moral feelings which he alone of terrestrial beings is capable of entertaining; and which tend to develope that self-directing power which becomes the instrument, when rightly employed, of all his noblest achievements.—The relation of the different parts of this highest form of the Nervous System to each other, and of the Will to the whole, may be made more clear by the following Table; which represents the ordinary course of its operation, when in a state of complete functional activity, and at the same time shows the character of the reflex activity which each part displays, when *it* is the highest centre that the impression can reach.


THE WILL
Intellectual Operations
Emotions
Ideas
Sensations
Impressions
CEREBRUM
centre of *emotional* and *ideo-motor* reflexion
SENSORY GANGLIA
centre of *sensori-motor* reflexion
SPINAL CORD
centre of *excito-motor* reflexion
Motor Impulse

The general rule of action appears to be, that the impressions made by external objects upon the afferent nerves, when transmitted to the Spinal Cord, ascend towards the Cerebrum, without exciting any 'reflex' movements in their course. When such an *impression* arrives at the Sensorium, it excites the consciousness of the individual, and thus gives rise to a *sensation;* and the change thus induced, being further propagated from the Sensory ganglia to the Cerebrum, gives occasion to the formation of an *idea.* If with this idea, any pleasurable or painful *feeling* should be associated, it assumes the character of an *emotion;* and the primary idea, with or without emotional complication, becomes the subject of *intellectual operations,* whose final issue is in a volitional determination, or act of the Will, which may be exerted either in producing or in checking a muscular movement, or in controlling or directing the current of thought.—But if this *upward* course be anywhere interrupted, the impression will then exert its power in a *transverse* direction, and a 'reflex' action will be the result, the nature of this being dependent upon the part of the Cerebro-Spinal axis, at which its ascent had been checked. Thus, if the interruption be produced by injury or division of the Spinal Cord, so that its lower part is cut-off from communication with the Encephalic centres, this portion then acts as an independent centre; and impressions made upon it through the afferent nerves proceeding to it from the lower extremities, excite violent movements, although they call forth no sensation; movements thus prompted are hence designated *excito-motor.* Such, we have every reason to believe, must be the character of nearly all the movements of those animals, whose nervous centres correspond rather to the Spinal Cord of Vertebrata, than to any higher portions of their system. If, again, the impression should reach the Sensorium, but should be prevented by the removal of the Cerebrum, or by its state of functional inaction, or by the direction of its activity into some other channel, from calling that organ into use, it may react upon the motor apparatus through the Sensory ganglia themselves; producing 'reflex' actions of the class that may be termed *sensori-motor* or *consensual*, since they cannot be excited, unless the consciousness be at the same time affected by the impression. This, too, will be the ordinary *modus operandi* of the Nervous System of those animals, which have scarcely any rudiment of a Cerebrum; and the 'excito-motor' and 'sensori-motor' actions together form that group, to which the term *Instinctive* is commonly applied.—But, further, if the Cerebrum should be in a state of activity, but the Will be in abeyance, *it* too responds automatically to any stimulus which it may receive from the Sensory Ganglia; ideas and emotions, either directly resulting from that impression, or called-up by the psychical changes which it may excite, express themselves in action without any volitional direction or restraint; and the course of thought, and consequently of conduct, is thus governed entirely by external influences, whose action on the system is *ideo-motor*. Such, there is strong reason to believe, is the condition of those Vertebrated animals which most nearly approach Man; for these, although unquestionably possessing a high degree of Intelligence, do not appear to exert any purely-volitional power over the workings of their minds, which seem to correspond exactly to those that take place automatically in ourselves, when the domination of the Will is temporarily or permanently suspended.

696. In tracing the progressive complication of the Psychical manifestations, during the early life of the Human being, a remarkable correspondence may be observed with that gradual increase in mental endowments, which is to be remarked in ascending the Animal scale. The first movements of an Infant are evidently of a purely automatic character, and are directed solely to the supply of its physical wants; they are thus analogous to the instinctive actions of the lowest animals possessed of a nervous system. The new sensations which are constantly being excited by surrounding objects, call into exercise the dormant powers of mind; notions are acquired of the character and position of external objects; and the simple processes of association, with its concomitant—memory, are actively engaged during the first months of an infant's life. At the same time an attachment to persons and places begins to manifest itself. All these are the characteristics of the great majority of the lower Vertebrata, so far, at least, as our knowledge of their springs of action enables us to form a judgment. As the child advances in age, the powers of observation are strengthened; the perceptions become more distinct; those powers of reflection are called-out which prompt him to reason upon the causes of what he observes, and his growing intelligence enables him to direct his actions to the attainment of objects of his desires; and at the same time we observe the development of moral feelings, which are at first manifested only towards beings who are the objects of sense. Among the more sagacious quadrupeds, it is easy to discover instances of reasoning as close and prolonged as that which usually takes place in early childhood; and the attachment of the dog to

man is evidently influenced by moral feelings, of which the latter is the object. "Man," it was expressively said by Burns, "is the God of the dog." Up to this point, then, we observe nothing peculiar in the character of Man; and it is only when he becomes capable of directing his course of thought and action by a strictly-volitional determination, and when his higher intellectual and moral endowments begin to manifest themselves, especially those relating to an invisible Being, that we can point to any obvious distinction between the immortal ψυχη of man, and the transitory πνευμα of the brutes that perish. May we not regard *these* endowments as *here* existing but as the germs or rudiments of those higher and more exalted faculties which the Human mind shall possess, when, purified from the dross of earthly passions, and enlarged into the comprehension of the whole scheme of Creation, the soul of Man shall reflect, without shade or diminution, the full effulgence of the Love and Power of its Maker?

[In the foregoing outline of the Structure and Actions of the Nervous System, the Author has simply aimed to express his own present convictions, and not to trace the history of the enquiry. He deems it but just, however, to state, that, although he has been led to abandon some parts of Dr. Marshall Hall's system of doctrines, which he formerly embraced, he still regards the results of that gentleman's enquiries as worthy of a place among the most important physiological discoveries of any age. In his progress towards what he now believes to be the true view of the relation of the Spinal Cord and its nerves to the Cerebrum, he has been partly guided by the views of Messrs. Todd and Bowman; from whom, however, he dissents, in regarding the Sensory Ganglia as parts of the Automatic apparatus, and in assigning to them functions altogether independent of the Cerebrum. His views on this subject were formed as far back as the year 1837; and were expressed in a paper, "On the Voluntary and Instinctive Actions of Living Beings," published in the "Edinb. Med. and Surg. Journ." No. CXXXII. In his general ideas of the relations of the different modes of nervous activity, and of their predominance in different tribes of animals respectively, he finds himself in close and unexpected accordance with Unzer, whose work entitled "Erste Gründe einer Physiologie der eigentlichen thierischen Natur thierischer Körper," published in 1771, displays an insight into the physiology of the Nervous System, which is the more wonderful, when the imperfect state of Anatomical knowledge (and especially of Comparative Anatomy) at that period is borne in mind.—The whole of the latter portion of the subject, and especially the relation of the Will to the Automatic activity of the Cerebrum, will be found much more fully discussed in the Author's "Human Physiology," 4th Edit. Chap. XIV., Sect. 5.]

CHAPTER XIV.

OF SENSATION, AND THE ORGANS OF SENSE.

1. *Of Sensation in General.*

697. It seems probable that all Animals which possess a definite Nervous System, have a greater or less degree of *consciousness* of the impressions made upon it, whether by external objects, or by changes taking place in their own organism; and to this consciousness, we give the name of *sensibility.* It is very important to bear in mind, however, that although we commonly refer our sensations to the parts on which the impressions are made, and speak of these parts as possessing sensibility, we really use incorrect language; since that of which we are actually conscious, is the change in the central *sensorium,* resulting from the excitement of its nervous polarity by the force transmitted from the periphery; and the difference between what are called 'sensible' and 'in-

sensible' parts of the body consists in this, that the former can receive and transmit the impressions which thus arouse the consciousness, whilst the latter are unable to do so. This is evident from two facts; *first*, that if the nervous communication of any 'sensible' part with the sensorium be interrupted, no impressions, however violent, can make themselves felt; and *second*, that if the trunk of the nerve be irritated or pinched, anywhere in its course, the pain which is felt is referred, not to the point injured, but to the surface to which these nerves are distributed. Hence the well-known fact, that, for some time after the amputation of a limb, the patient feels pains, which he refers to the fingers or toes that have been removed; this continues, until the irritation of the cut extremities of the nervous trunks has subsided.

698. It would seem probable that, among the lower tribes of Animals, there exists no other kind of sensibility than that termed 'general' or 'common;' which exists, in a greater or less degree, in almost every part of the bodies of the higher. It is by this, that we feel those impressions, made upon our bodies by the objects around us, which produce the various modifications of pain, the sense of contact or resistance, and others of a similar character. From the dependence of the impressibility of the sensory nerves upon the activity of the circulation in the neighbourhood of their extremities, it is obvious that no parts destitute of blood-vessels can receive such impressions, or (in common language) can possess sensibility. Accordingly we find that the Hair, Nails, Teeth, Cartilages, and other parts that are altogether extravascular, are themselves destitute of sensibility; although certain parts connected with them, such as the bulb of the hair, or the vascular membrane lining the pulp-cavity of the tooth, may be acutely sensitive. Again, in Tendons, Ligaments, Fibro-cartilages, Bones, &c., whose substance contains very few vessels, there is but a very low amount of sensibility. On the other hand, the Skin and other parts, which are peculiarly adapted to receive such impressions, are extremely vascular; and it is interesting to observe, that some of the tissues just mentioned become acutely sensible, when new vessels form in them in consequence of diseased action. It does not necessarily follow, however, that parts should be sensible in a degree proportional to the amount of blood they may contain; for this blood may be sent to them for other purposes, and they may contain but a small number of sensory nerves. Thus, it is a condition necessary to the action of Muscles, that they should be copiously supplied with blood; but they are by no means acutely sensible; and, in like manner, Glands, which receive a large amount of blood for their peculiar purposes, are far from possessing a high degree of sensibility.

699. But besides the 'general' or 'common' sensibility, which is diffused over the greater part of the body, there are certain parts in most animals, which are endowed with the property of receiving impressions of a peculiar or 'special' kind, such as sounds or odours, that would have no influence on the rest; and the sensations which these excite, being of a kind very different from those already mentioned, arouse ideas in our minds, which we should never have gained without them. Thus, although we can acquire a knowledge of the shape and position of objects by the touch, we could form no notion of their colour without sight, of their sounds without hearing, or of their odours without smell. The

nerves which convey these 'special' impressions, are not able to receive those of a 'common' kind; thus the eye, however well fitted for seeing, would not feel the touch of the finger, if it were not supplied by branches from the Fifth pair, as well as by the Optic. Nor can the different nerves of 'special' sensation be affected by impressions that are adapted to operate on others; thus the Ear cannot distinguish the slightest difference between a luminous and a dark object; nor could the Eye distinguish a sounding body from a silent one, except when the vibrations can be *seen*. But Electricity and other Physical Forces, when applied to the several nerves of special sense, may excite the sensations peculiar to each respectively.

700. It is further important to keep in mind the distinction between the *sensations* themselves, and the *ideas* which are the immediate results of those sensations, when they are perceived by the mind. These ideas relate to the *cause* of the sensation, or the object by which the impression is made. Thus, the formation of the picture of an object upon the retina, produces a certain impression upon the optic nerve; which, being conveyed to the sensorium, excites a corresponding sensation; and with this, in all ordinary cases, we immediately connect an idea of the nature of the object. So closely, indeed, is this idea usually related to the sensation, that we are not in the habit of making a distinction between the two. We find that some of these *perceptions* or elementary notions are *intuitive;* that is, they are prior to all experience, and are as *necessarily* connected with the sensation which produces them, as 'reflex' movements are with the impression that excites them. This seems to be the case, for example, with regard to *erect vision*. There is no reason whatever to think, that either infants or any of the lower animals see objects in an inverted position, until they have corrected their notion by the touch; for there is no reason why the inverted picture on the retina should give rise to the idea of the inversion of the object. The picture is so received by the mind, as to convey to us an idea of the position of external objects, which harmonizes with the ideas we derive through the touch; and whilst we are in such complete ignorance of the manner in which the mind becomes conscious of the sensation at all, we need not feel any difficulty about the mode in which this conformity is effected. But in Man, the attaching definite ideas to certain groups of lines, colours, &c., with respect to the objects they represent, is a subsequent process, in which experience and memory are essentially concerned; as we see particularly well, in cases of no unfrequent occurrence, in which the sense of sight has been acquired comparatively late in life, and in which the mode of using it, and of connecting the sensations received through it with those received through the touch, has had to be learned by a long-continued training. The elementary notions thus formed, which may, by long habit, present themselves as immediately and unquestionably as if they were intuitive, are termed *acquired* perceptions.

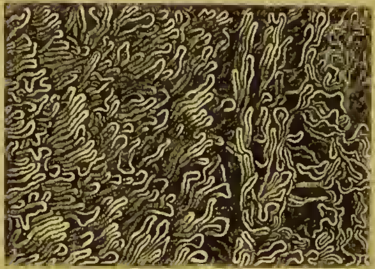
701. It is probable that, among the lower animals, the proportion of *intuitive* perceptions is much greater than in Man; whilst, on the other hand, his power of acquiring perceptions is much greater than theirs. So that, whilst the young of the lower animals very soon become possessed of all the knowledge, which is necessary for the acquirement of their food, the construction of their habitations, &c., their range is very

limited, and they are incapable of attaching any ideas to a great variety of objects, of which the human mind takes cognizance. This correspondence between the 'acquired' perceptions of Man, and the 'intuitive' perceptions of many of the lower animals, is strikingly evident in regard to the power of measuring distance; which is acquired very gradually by the Human infant, or by a person who has first obtained the faculty of sight later in life; but which is obviously possessed by many of the lower animals, to whose maintenance it is essential, immediately upon their entrance into the world. Thus a Flycatcher, immediately after its exit from the egg, has been known to peck-at and capture an insect,—an action which requires a very exact appreciation of distance, as well as a power of precisely regulating the muscular movements in accordance with it.

2. *Of the Sense of Touch.*

702. By the sense of Touch is usually understood that modification of the common sensibility of the body, of which the surface of the Skin is the especial seat, but which exists also in some of its internal reflexions. In some animals, as in Man, nearly the whole exterior of the body is endowed with it, in no inconsiderable degree; whilst in others, as the greater number of Mammalia, most Birds, Reptiles, and Fishes, and a large proportion of the Invertebrata, the greater part of the body is so covered with hairs, scales, bony or horny plates, shells of various kinds, complete horny envelopes, &c., as to be nearly insensible; and the faculty is restricted to particular portions of the surface, or to organs projecting from it, which often possess a peculiarly high degree of this endowment. Even in Man, the acuteness of the sensibility of the cutaneous surface varies much in different parts; being greatest at the extremities of the fingers, and in the lips; and least in the skin of the trunk, arm, and thigh.

Fig. 289.



Distribution of Capillary blood-vessels in *Cutaneous Papillæ*.

703. The impressions that produce the sense of Touch, are ordinarily received through the sensory *papillæ*, which are minute elevations of the surface, enclosing loops of capillary vessels (Fig. 289), and filaments of the sensory nerves.—True papillary organs have not yet been discovered in any Invertebrata; nor even in Fishes, Serpents, or Chelonians.—In the soft-skinned *Batrachia*, an imperfect papillary structure is extensively diffused over the surface; but on the thumb of the male Frog, and probably on that of other Batrachia, large papillæ are developed at the season of sexual excitement. In many Lizards, a papillary structure is found on the under surface of the toes; and in the Chameleon it exists also in the integuments of its prehensile tail.—In Birds, the only parts of the skin on which tactile papillæ seem to exist, are the under surface of the toes, and the web of the Palmipedes, on which sensory impressions are made that guide the movements of the feet; and the bill of the Duck tribe, which is plunged into the mud, &c., in search of food.—Among Mammalia, we find that the papillary structure is especially developed on those parts of the tegumentary surface, which

are of the most important use in appreciating the qualities of the food, or in guiding the movements of the instruments of locomotion. Thus in the Quadrumana generally, both hands and feet are thickly set with papillæ; and in those which have a prehensile tail, the surface of this organ possesses them in abundance. In the Carnivorous and Herbivorous Mammals, whose extremities are furnished with claws or encased in hoofs, we find the lips and the parts surrounding the nostrils to be the chief seat of tactile sensibility, and to be copiously furnished with papillæ; and this is especially the case with those, which have the lips or nostrils prolonged into a snout or proboscis, as the Pig, the Rhinoceros, the Tapir, and the Elephant. In the Mole, too, the papillary structure is remarkably developed at the end of the snout.—The papillary apparatus, and the sense to which it ministers, are not confined, however, to the tegumentary surface of the exterior of the body; for we find that the tongue of many animals is copiously furnished with sensory papillæ; and it is probable, from the experience of Man, that only a part of these minister to the sense of Taste, but that the remainder are tactile (§ 706).

704. A very different set of instruments is developed for this sense, however, in certain animals; either in place of, or in addition to, the true papillary apparatus. Thus, in Articulated animals generally, the jointed appendages to the head, known as *antennæ* and *palpi*, are undoubtedly instruments of touch; and this function they may execute most efficiently, notwithstanding the density of their covering. For just as a blind man judges of the proximity and characters of objects, by the impressions communicated to his hand by the contact of the stick with which he examines them, so may an Insect or a Crustacean receive sensory impressions upon the nerves distributed to the basal joints of their long antennæ, although the organs themselves may be as insensible (or rather, as unimpressible) as the stick.* The antennæ, when prolonged, seem to guide the movements of the animal; whilst, on the other hand, the palpi rather appear to minister to the cognizance of objects brought into the neighbourhood of the mouth, and to have for their chief office to guide in the selection of food.—In many of the higher animals, the *hairs* are most delicate instruments of touch; for although themselves insensible, their bulbs are seated upon cutaneous papillæ, copiously provided with nerves and blood-vessels, in such a manner that any motion or vibration communicated to the hair must produce an impression upon the papilla at its base. Such an organisation is found in those long stiff hairs, which are known as the *vibrissæ* or 'whiskers' of the Feline tribe, and which are particularly large in the Seal. These sensitive hairs are also highly developed in many of the Rodentia, such as the Hare and Rabbit; and it has been proved by experiment, that, if they

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* The Author is acquainted with a blind gentleman, who exhibits a remarkable dexterity in the use of his stick in guiding his movements; and has been informed by him, that much of his power of discrimination depends upon the flexibility, elasticity, &c. of this instrument; so that, when he has chanced to lose or break the one to which he has been accustomed, it is often long before he can obtain another that shall suit him as well.—This circumstance seems to throw some light upon the remarkable variety which is seen in the conformation of the *antennæ* of Insects; as it may be imagined that each is adapted to receive and to communicate impressions of a particular class, adapted to the wants of the species.

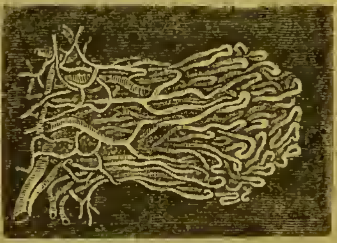
be cut-off, the animal loses in great degree its power of guiding its movements in the dark.

705. The only idea communicated to our minds, when the sense of Touch is exercised in its simplest form, is that of *resistance;* and we can neither acquire a notion of the size or shape of an object, nor judge correctly as to the nature of its surface, through this sense alone, unless we *move* the object over our own sensory organ, or pass the latter over the former. By the various degrees of resistance which we then encounter, we form our estimate of the hardness or softness of the body. By the impressions made upon our sensory papillæ, when they are passed over its surface, we form our idea of its smoothness or roughness. But it is through the *muscular* sense, which renders us cognizant of the relative position of the fingers, of the amount of movement the hand has performed in passing over the object, and of other impressions of like nature, that we acquire our notions of the size and figure of the object; and hence we perceive that the sense of Touch, without the power of giving motion to the tactile organ, would have been of comparatively little use. It is chiefly in the *variety* of movements, of which the hand of Man is capable,—thus conducive as they are, not merely to his prehensile powers, but to the exercise of his sensory endowments,—that it is superior to that of every other animal; and it cannot be doubted, that this affords us a very important means of acquiring information in regard to the external world, and especially of correcting many vague and fallacious notions, which we should derive from the sense of Sight, if used alone. The power of *tactile discrimination* does not by any means bear a constant relation to the degree of 'common sensibility' in a part, that is, to its susceptibility to impressions which produce pain; for the latter may depend simply upon the amount of nerves supplied to the surface; and this may be great in parts which have few papillæ, and which are supplied by nerves whose central terminations are so closely blended, that impressions made on points which are in near approximation to each other cannot be distinguished. The sensory apparatus contained in the integuments would seem to be necessary for the exercise of the *sense of temperature;* for it appears from the recent experiments of Prof. Weber, that if the integuments be removed, the application of hot or cold bodies only causes *pain,* their elevation or depression of temperature not being perceived; and the same is the case, when hot or cold bodies are applied to the nerve-trunks. It is worthy of note that there are many cases on record, in which the sense of Temperature has been lost, whilst the ordinary Tactile sense remains; and it is sometimes preserved, when there is a complete loss of every other kind of sensibility. So again we find that the *subjective* sensations of temperature,—that is, sensations which originate from changes in the body itself, not from external impressions,—are frequently excited quite independently of those of contact or resistance; a person being sensible of heat or chilliness in some part of his body, without any real alteration of its temperature, and without any corresponding affection of the tactile sensations. And further, it is to be remarked, that whilst, for the exercise of the Tactile sense, absolute *contact* between the impressible surface and the solid body is required, the influence of temperature may be communicated by radiations from a distance.

3. *Of the Sense of Taste.*

706. The sense of Taste, like that of Touch, is excited by the direct contact of particular substances with certain parts of the body: but it is of a much more refined nature than touch; inasmuch as it communicates to us a knowledge of properties, which that sense would not reveal to us. All substances, however, do not make an impression on the organ of Taste. Some have a strong savour, others a slight one, and others are altogether insipid. The cause of these differences is not altogether understood; but it may be remarked that, in general, bodies which cannot be dissolved in water, alcohol, &c., and which thus cannot be presented to the gustative papillæ in a state of solution, have no taste. A considerable part of the impression produced by many substances taken into the mouth, is received through the sense of Smell, rather than through that of Taste. There are many substances, however, which have no aromatic or volatile character; and whose taste, though not in the least dependent upon the action of the nose, is nevertheless of a powerful character.—The sense of Taste has for its chief purpose, to direct animals in their choice of food; hence its organ is always placed at the entrance to the digestive canal. In higher animals, the Tongue is the principal seat of it; but other parts of the mouth are also capable of receiving the impression of certain savours. The mucous membrane which covers the tongue, is copiously supplied with papillæ, of various forms and sizes. Those of simplest structure closely resemble the Cutaneous papillæ; but there are others, which resemble clusters of such papillæ, each being composed of a fasciculus of looped capillaries (Fig. 290), with a bundle of nerve-fibres, whose precise mode of termination it has not yet been found possible to ascertain. These *fungiform* papillæ, which are covered with a very thin epithelium, are probably the special instruments of the sense of taste; for the exercise of which it seems probable that the sapid substance should penetrate (in solution) to the interior of the papilla.—The *conical* papillæ, on the other hand, being furnished with thick epithelial investments, which are sometimes prolonged into horny spines, would seem destined chiefly to mechanical purposes; thus in the Felines, in which tribe the spines are most remarkably developed, they form a most efficient rasp, by which the bones of their prey may be stripped of the smallest particles of flesh that may adhere to them; and in other cases, in which the investments are rather of a brush-like nature, they probably serve to cleanse the teeth from adhering particles, whilst the tactile sensibility of the papillæ directs the muscular movements of the tongue.—Of the degree of Taste possessed by different animals, it is impossible to form an accurate judgment, without a more accurate means of discrimination than we possess, between the Gustative and Tactile papillæ of the tongue. And we have not any certain knowledge, how far the sense of Taste may be exercised without a papillary structure.

Fig. 290.



Capillary plexus of *fungiform papilla* of Human Tongue.

4. *Of the Sense of Smell.*

707. Certain bodies possess the property of exciting sensations of a peculiar nature, which cannot be perceived by the organs of taste or touch, but which seem to depend upon the diffusion of the particles of the substance through the surrounding air, in a state of extreme minuteness. As the solubility of a substance in liquid seems a necessary condition of its exciting the sense of taste, so does its volatility, or tendency to a vaporous state, appear requisite for its possession of Odorous properties. Most volatile substances are more or less odorous; whilst those which do not readily transform themselves into vapour, usually possess little or no fragrance in the liquid or solid state, but acquire strong odorous properties as soon as they are converted into vapour,—by the aid of heat, for example. There are some solid substances, which manifest very strong odorous properties, without losing weight in any appreciable degree by the diffusion of their particles through the air. This is the case, for example, with Musk; a grain of which has been kept freely exposed to the air of a room, whose door and windows were constantly open, for a period of ten years; during which time the air, thus continually changed, was completely impregnated with the odour of musk; and yet, at the end of that time, the particle was not found to have perceptibly diminished in weight. We can only attribute this result to the extreme minuteness of the division of the odorous particles of this substance. There are other odorous solids, such as Camphor, which rapidly lose weight by the loss of particles from their surface, when freely exposed to the air.

708. The conditions of the sense of Smell are best studied in the higher animals. The membrane over which the olfactive nerve is distributed, is extremely vascular, and is covered with a thick pulpy epithelium; and the nerves lose themselves in its substance, apparently becoming divested of the 'white substance of Schwann,' and presenting a close resemblance to the 'gelatinous' fibres. The odoriferous medium must be brought into contact with this surface; and the surface itself must be neither dry, nor clogged with too large an amount of fluid secretion.—How far any sense of smell exists in the lower Invertebrata, cannot be satisfactorily determined; but it would seem not improbable, that even where no special organ is apparent, some part of the general surface may be endowed with Olfactive sensibility. In the *Pulmoniferous Gasteropods,* which seem guided to their food by its scent, there is strong ground to regard the extremities of the larger tentacula (which bear the eyes near their points) as special organs of smell;* and the dorsal tentacula of the *Nudibranchiata,* which frequently have a peculiar laminated structure, are probably to be regarded in the same light.† In the *Bullidæ,* which have no proper tentacles, the head-lobes receive the nerves (proceeding from the anterior portion of the cephalic ganglia) which are elsewhere transmitted to the olfactive tentacles;‡ and in *Bulla hydatis* we find these nerves terminating in a peculiar organ, composed of a central stem bearing numerous lateral laminæ, which forms a complete link of

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* See Moquin-Tandon, in "Ann. des Sci. Nat.," 3e Sér., Zool., Tom. XV., p. 151.

† See Embleton, in "Ann. of Nat. Hist." 2nd Ser., Vol. III., p. 193.

‡ See Hancock, Op. cit., Vol. IX., p. 188.

connection between the laminated tentacles of *Doris*, and the olfactive organ of Fishes. A similar organ has been described by Prof. Owen in *Nautilus;* but none such has yet been detected in the *Dibranchiate Cephalopods.*—Among the higher Articulata, there is ample reason to believe that the sense of Smell exists, although there is considerable uncertainty regarding its special instrument. That many *Insects* are guided to their food, to the proper nidus for their eggs, and to the opposite sex of their own species, and are even informed of the proximity of their natural enemies, by odorous emanations, can scarcely be doubted by any one who has watched their habits and experimented upon their actions. Some Entomologists have supposed the seat of the olfactory sense in Insects to be in their antennæ, others in the palpi, and others in the entrances to their tracheæ. The latter supposition must be considered as very improbable; and it derives no real support from experiment, since the movements which may be produced in a decapitated insect, by bringing acrid vapours into proximity with the stigmata, are evidently analogous to those of coughing and sneezing, which similar acrid vapours excite in Man, not through the sense of Smell, but through the 'common' sensibility of the membrane lining the respiratory passages. It is very difficult to determine by experiment, whether the antennæ or the palpi are the most probable instruments of the olfactive sense; and it seems not unlikely that, as the antennæ and palpi are appendages of a similar class, the sense of Smell may not be constantly localized in either of them, but that it may be assigned to one or to the other, according to the modifications they respectively require for the performance of their other offices.*—The same may be stated in regard to the olfactive organ of the *Crustacea.* The manner in which Crabs and Lobsters are attracted by odorous bait placed in closed traps, makes it almost certain that they must possess some sense of Smell; and there can be little doubt that its instrument will be found in the basal joint of either the first or the second pair of antennæ.†

709. The Olfactive organ of Vertebrata usually corresponds with that of Man in its general characters: but whilst, in all air-breathing Vertebrata, it may be considered as a diverticulum from the commencement of the respiratory tube,—being obviously placed there, not only in order that the respiratory current may effectually introduce the odoriferous medium, but also that it may serve to warn its possessor of the presence of such odoriferous emanations as cannot be breathed with impunity,—in *Fishes* its cavity is not connected with the respiratory passages, and has no posterior nares, its sole orifice being in front. Within this cavity, however, the olfactive surface is greatly extended, by the leaf-like plication of the pituitary membrane; and the water introduced into it is continually renewed by the action of the cilia with which that membrane is beset. In the Sharks and Rays, moreover, there is a muscular apparatus for more rapidly changing the current of water within the olfactory sac;

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* See MM. Perris and Léon-Dufour, in "Ann. des Sci. Nat.," 3e Sér., Zool., Tom. XIV.

† It has been customary to regard, with Rosenthal, the sacculus in the first pair of antennæ as the olfactive organ, and that in the second as the auditory organ. Dr. A. Farre, however, has adduced strong reasons for reversing this opinion ("Philosophical Transactions," 1843); and Mr. Huxley has adopted and strengthened Dr. Farre's views (§ 712).

whence, as Prof. Owen remarks, we must conclude that these Fishes *scent* (*i. e.*, actively search for odoriferous impressions), as well as smell. In *Reptiles* there is but little provision for the extension of the olfactive surface; and there is no evidence that the sense of Smell is more than very feebly developed in them. In *Birds*, the nasal cavity is of considerable size, and its lining membrane is spread over the 'turbinated bones,' which project into its cavity; still there is reason to believe that much of what has been set down to the account of Smell in Birds, is really attributable to their acute sight, and that in no Birds is there any approach in this respect, to those Mammals which are most distinguished for the acuteness of their scent. The organ of Smell in *Mammalia* is for the most part highly developed, the nasal cavity being large, and the surface over which the olfactive nerve is distributed being augmented by the convolution of the 'turbinated bones.' Of these bones, the lowest is the one that is usually most developed; and in the Carnivora, to which animals this sense is of the greatest importance in guiding them to their prey, this bone is divided into a number of irregular lateral laminæ, so that a transverse section of it has an arborescent form. The nasal cavity is usually more or less extended by sinuses, which communicate with large cancelli in the surrounding bones; so that the olfactive organs are far more highly developed in most of the lower Mammalia than they are in Man, serving not merely to guide the Carnivora to their prey, but to warn the timid Herbivora of the approach of their enemies, and being probably one of the chief means whereby the opposite sexes are made aware of each other's proximity. In the order *Cetacea*, however, the turbinated bones are altogether wanting, and neither olfactive ganglia nor nerves are developed; so that among these animals, the sense of Smell, which could not be very efficiently exercised in the water, seems to be sacrificed to two objects more particularly connected with their general organisation and habits,—namely, the reception of air into the lungs, whilst the head and body are immersed in water; and the ejection of water which has been received into the mouth with the food, but which the animal does not require to swallow.

5. *Of the Sense of Hearing.*

710. By this sense we become acquainted with the sounds produced by bodies in a certain state of vibration; the vibrations being propagated through the surrounding medium, by the corresponding waves or undulations which they produce in it. Although air is the usual medium through which sound is propagated, yet liquids or solids may answer the same purpose. On the other hand, no sound can be propagated through a perfect vacuum.—It is a fact of much importance, in regard to the action of the Organ of Hearing, that sonorous vibrations which have been excited, and are being transmitted, in a medium of one kind, are not imparted with the same readiness to others. The following conclusions have been drawn from experimental inquiries on this subject.

I. Vibrations excited in *solid* bodies, may be transmitted to *water* without much loss of their intensity; although not with the same readiness that they would be communicated to another solid.

II. On the other hand, vibrations excited in *water* lose something of their intensity in being propagated to *solids;* but they are returned, as it were, by these solids to the liquid, so that the sound is more loudly heard in the neighbourhood of these bodies, than it would otherwise have been.

III. The sonorous vibrations are much more weakened in the transmission of *solids* to *air;* and those of *air* make but little impression on *solids.*

IV. Sonorous vibrations in *water* are transmitted but feebly to *air;* and those which are taking place in *air* are with difficulty communicated to *water;* but the communication is rendered more easy, by the intervention of a membrane extended between them.

The application of these conclusions, in the Physiology of Hearing, will be presently apparent.

711. The essential part of an Organ of Hearing is a nerve endowed with the peculiar property of receiving and transmitting sonorous undulations; and it is by no means indispensable that any other special provision should be made for this purpose, since the Auditory nerve may be spread out over any surface which will be affected by the undulations of the surrounding medium. Hence we must not imagine the sense to be absent, wherever we cannot discover a definite organ for the purpose. On the other hand, we are not to suppose that animals possess a distinct auditory sense, merely because we find them possessed of organs homologous with those which are certainly the instruments of that sense in higher animals; for they may be so rudimentary in their degree of development, that we can scarcely imagine them to possess any considerable functional capacity. Such is the case with regard to the *Acalephæ*, the lowest animals in which any such organs have been detected. At regular intervals along the margin of the disk, in most kinds of *Medusæ* and their allies (Fig. 36, *f, f*), there may be found a series of peculiar sacculi, containing either a single large highly-refracting spheroidal body, or a collection of calcareous granules; both these forms having such precise representatives in the auditory organs of Mollusca, that the similarity of their nature can scarcely be doubted, more especially as the peculiar vibratory movement which characterizes the latter has been witnessed also in the former.* Of the existence of auditory organs among the *Tunicated* Mollusks, there can scarcely be any reasonable doubt. In *Chelyosoma*, one of the simple *Ascidians*, a vesicular body in immediate connection with the single nervous ganglion, has been described by Eschricht as an auditory organ; and it is probable that the single or double tubercular body which has been described by Savigny as existing in the same situation, in various Ascidians both simple and compound, has the same character. The auditory nature of this organ is still more obvious in the *Salpæ;* in which it is described by Mr. Huxley as a strong transparent vesicle, attached to the nervous ganglion, and containing four hemispherical bodies, with black pigment-spots upon their outer surface; whilst

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* The auditory nature of these organs, which had been previously considered to be rudimentary Eyes, was first asserted by Will, in his "Horæ Tergestinæ," 1844; who has been since supported by Kölliker and Huxley. Mr. G. Busk, on the other hand, has sustained their visual character ("Microscopical Transactions," Vol. III., pp. 24, *et seq.*); but he seems not to have been aware how closely they are paralleled among the Mollusca; nor had he distinguished the ciliary movement within the capsule, which has been not only observed by Kölliker ("Froriep's Neue Notizen," No. 534), but also by Mr. Huxley, as that gentleman has himself informed the Author.

a conical depression in the outer tunic leading towards this vesicle, would appear to be intended to bring it into closer relation with the surrounding medium.* Among the Lamellibranchiata, or such (at least) as possess a foot, a pair of similar vesicles is found at the base of that organ, either sessile upon the pedal ganglion, or connected with it by nervous peduncles; and the calcareous concretions or 'otolithes' they contain (which are of a vitreous aspect and crystalline structure) execute continual vibratory and rotatory movements, which immediately cease on the rupture of the capsule.† The development of these organs is but little more advanced in the *Gasteropoda,* among which they are usually found situated, either in immediate apposition with the pedal ganglia that form the principal part of the subœsophageal portion of the nervous collar, or connected with these ganglia by short peduncles. In *Nudibranchiata,* however, they have a higher position, though they still accompany the pedal ganglia, which are found in those animals united with the cephalic ganglia above the œsophagus; and in *Heteropoda,* the auditory organs appear to be connected with the cephalic ganglia, though this (as Mr. Huxley has suggested) may not be the case in reality. Each auditory capsule may contain but a single otolithe, which is then spherical and of crystalline aspect, or it may include a large number of minute fusiform particles; the movements of these bodies, which are extremely active, have been ascertained to be due to the vibration of the cilia which clothe the epithelium lining the capsules.‡ In the *Cephalopoda,* we find the auditory sac of each side detached from the ganglionic mass, with which it remains connected by the auditory nerve; and the sac itself, which contains a single 'otolithe' of irregular form, is lodged in a cavity excavated in the cartilage that supports the cephalic nervous centres; an arrangement that evidently foreshadows the proper 'sense-capsule,' which it acquires in Vertebrata. No greater degree of complexity, however, is attained by the instrument itself, notwithstanding the close approximation which Cephalopods present to Vertebrata in the general elaborateness of their organisation.

712. There can be no doubt that the lower *Articulata* possess the sense of Hearing, although its special organ cannot always be detected. In certain *Annelida,* however, M. de Quatrefages has detected auditory capsules with otolithes, exactly resembling those of Mollusks.§ It is obvious that the movements of *Insects* are guided by hearing, the sexes being frequently attracted to each other by the sounds which one of them has the power of producing; and it is probable that the organ of this sense is enclosed in the basal joints of the antennæ.|| In *Crustacea* its presence seems much less equivocally indicated; and yet it appears probable from recent enquiries, that what has been usually considered the

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* "Philos. Transact.," 1851, p. 571.

† The true nature of these organs, which, though they had been noticed by many Anatomists, had not been understood, was first recognized by Prof. Siebold, from their correspondence with the Auditory capsules in the early embryo of Fishes. See "Müller's Archiv.," 1838, and "Wiegmann's Archiv.," 1841; also "Ann. des Sci. Nat.," 2e Sér., Zool., Tom. X., XIX.

‡ The existence of Auditory organs in this group was first recognized among the *Heteropoda* by MM. Eydoux and Souleyet ("L'Institut.," 1838, No. 255). For a *résumé* of the subsequent researches of various Anatomists, see Prof. Siebold's "Vergleichende Anatomie," Band I., § 211.

§ "Ann. des Sci. Nat.," 3e Sér., Zool., Tom. XIII., p. 29.

|| See MM. Perris and Léon-Dufour, loc. cit.

organ of Hearing (which is a cavity in the first joint of the *second* or larger pair of antennæ, having a round orifice closed by a membrane, and containing a vesicle filled with fluid, on which the antennal nerve expands), is in reality an organ of Smell, and that the true organ of Hearing is in the basal joint of the *first* or smaller pair of antennæ. For in *Lucifer*, as described by Mr. Huxley,* we find in this situation a sacculus containing a single spherical strongly-refracting otolithe, so closely resembling the organ of Hearing in Gasteropoda, that there can scarcely be a doubt of its analogous character; although it is completely enclosed in the crustaceous envelope of the member in which it is situated. In *Palæmon* there is a departure from this type, which leads us towards the ordinary form of the organ in Crustacea; for in the envelope of the basal joint of the antennæ is a narrow fissure, which opens into a pyriform cavity, contained within a membranous sac that lies within the substance of the joint. The anterior extremity of the sac is enveloped in a mass of pigment-granules; whilst on the side which is opposite to the fissure, a series of hairs with bulbous bases are attached, on which seems to rest a large ovoidal strongly-refracting otolithe. The antennal nerve gives-off branches which terminate at the bases of the hairs; and it can scarcely be doubted that it is through the vibrations of the otolithe transmitted to them, that the sonorous undulations are perceived.—The ordinary structure of the organ of hearing in the Macrourous Decapods, as described by Dr. A. Farre,† presents a very curious modification of this type. The auditory sac, enclosed in the basal joint of the smaller antennæ, communicates with the external surface by a small valvular aperture; and instead of calcareous 'otolithes,' particles of siliceous sand are found in its interior, which appear to have entered by this orifice. These, in the ordinary position of the animal, will rest upon the extremities of a row of hair-like processes, which project into the interior of the sac; and each of these processes contains a row of cells, which are probably nerve-vesicles. This sacculus is connected with the cephalic ganglia, by a nerve-trunk distinct from that which supplies the antenna itself; and this trunk forms a plexus which surrounds the sac, but which is peculiarly abundant beneath the row of hair-like processes. There can scarcely be a reasonable doubt of the Auditory nature of this organ, the connection between this and the more usual forms of the organ of hearing, being supplied by Palæmon and Lucifer; and it is interesting to find the place of otolithes here taken by particles of sand introduced from without,—a provision which reminds us (as Dr. A. Farre has justly remarked) of the introduction of stones into the stomach of Granivorous Birds, in which they answer the purpose of gastric teeth. A portion of the shell of the joint is unconsolidated in the lobster; so that the mouth of the auditory sac is only covered-in by a membrane, which may be considered as the representative of that which closes the 'fenestra ovalis' of the vestibule of Vertebrata; but in many other Decapods, the shelly covering is complete over the whole joint, save at the valvular orifice. The fluid of the auditory sac will be thrown into vibration by undulations of the surrounding medium, communicated either through the membrane covering the 'fenestra ovalis,' or through the shelly investment;

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* "Annals of Natural History," 2nd Ser., Vol. VII., p. 304.

† "Philosophical Transactions," 1843.

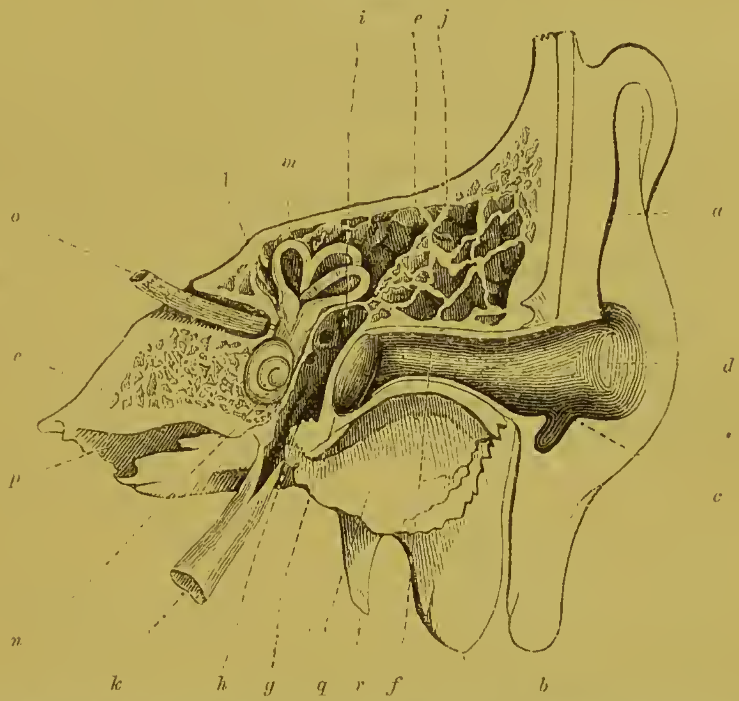
and the vibrations will be strengthened by the presence of the sandy particles, which also, there is reason to believe, will, by their own vibration, make stronger impressions upon the hair-like processes, than the liquid itself would do.—No special organ of hearing has yet been discovered in *Arachnida.*

713. A special organ of Hearing exists in all *Vertebrated* animals save the *Amphioxus;* but in the lowest Cyclostome Fishes, it presents little or no advance in its development, upon the type on which it is constructed in the Cephalopods. For it consists of a simple sac, lodged in the cranial cartilage, and having no direct external communication; this sac is filled with fluid, and contains otolithes; and the auditory nerve is distributed upon its walls. In ascending through the series of *Cyclostomi,* however, we find the 'semicircular canals' successively devoloped; only one of these passages being present in *Myxine,* two in the *Lamprey,* and three in all the higher members of the class. At the same time, provision is made for the more direct action of the sonorous undulations of the surrounding medium, upon the fluid contained in the auditory sac or labyrinth; for a portion of its investing cartilage or bone is deficient at one part of the external surface, the aperture being only closed by a membrane, through which the communication can readily take place. Some rudiments of a tympanic cavity, interposed between this membrane and the external surface, may be found in certain Osseous Fishes; and in several tribes, the organ of hearing possesses a peculiar connection with the air-bladder, which appears to be a foreshadowing of the 'Eustachian tube' of higher classes.—In the true *Reptiles,* a considerable advance is constantly to be found in the character of the Auditory organ; for a tympanic cavity is added, with a membranous 'drum' and a chain of bones; and a rudiment of a 'cochlea' is generally discoverable, which has a separate opening (fenestra rotunda) into the tympanic cavity. The 'membrana tympani' is usually visible externally, but it is sometimes covered by the skin; the cavity of the tympanum communicates with the fauces by an 'Eustachian tube.' Among the *Amphibia* there is a considerable variation in the structure of the organ of Hearing; for whilst some possess the tympanic apparatus, others are entirely destitute of it.—In *Birds,* the structure of the Ear is essentially the same as in the higher Reptiles. A distinct 'cochlea' always exists, though its form is not spiral, but nearly straight; and its cavity is divided into two passages by a membranous partition, on which the ramifications of the auditory nerve are spread-out. There is no external ear, save in a few species of nocturnal Birds; but the tympanic cavity communicates with cavities in the cranial bones, which are thus filled with air; and these, by increasing the extent of surface, produce a more powerful resonance.

714. In the ordinary *Mammalia,* the organ of Hearing is formed upon the same general plan as it presents in Man; though in the Monotremata, it more approaches that of Birds. All the Mammalia, save the aquatic tribes, have an external ear, and this is sometimes of an enormous size in proportion to the dimensions of the body, as is seen especially in the Bats. Moreover in several tribes it can be turned in any direction by muscular movement, so as most advantageously to receive the faintest sounds from any quarter. The canal (Fig. 291, *d*) into which the external ear reflects the sonorous vibrations, passes inwards

until it is closed by the *membrana tympani* or 'drum of the ear' (*g*), which forms the external wall of the tympanic cavity. Within this cavity, which communicates with the throat by the 'Eustachian tube' (*k*), there is a series of small bones, which serve to establish a connection between the membrana tympani and that which covers-in the 'fenestra ovalis.' The long handle of the 'malleus' is attached to the membrana tympani, and near its base it gives attachment to the 'tensor tympani' muscle; its head is received into a hollow on the body of the 'incus,' which also has a long process that is connected with the 'stapes;' whilst the oval extremity of the 'stapes' is attached to the membrane covering the 'fenestra ovalis,' or entrance to the labyrinth, this little bone being also connected with the minute 'stapedius' muscle, which regulates its movements.—The purpose of this Tympanic apparatus is evidently to receive the sonorous vibrations from the air, and to transmit them to the membranous wall of the labyrinth; in such a manner that the vibrations thus excited in the latter may be much more powerful, than they would be if the air acted immediately upon it, as in the lower Vertebrata. The usual condition of the membrana tympani appears to be rather lax; and, when in this condition, it vibrates in accordance with grave or deep tones. By the action of the 'tensor tympani' (a little muscle lodged in the Eustachian tube) it may be tightened, so as to vibrate in accordance with sharper or higher tones; but it will then be less able to receive the impressions of deeper sounds. This state we may easily induce artificially,

FIG. 291.



Vertical Section of the *Human Ear*, the internal portions on an enlarged scale;—*a*, *b*, *c*, external ear; *d*, entrance to auditory canal, *f*; *e*, *e*, petrous portion of temporal bone; *g*, membrana tympani; *h*, cavity of the tympanum, the chain of bones being removed; *i*, openings from this cavity into the cells, *j*, excavated in the bone; on the side opposite the membrana tympani are seen the fenestra ovalis and rotunda; *k*, Eustachian tube; *l*, vestibule; *m*, semicircular canals; *n*, cochlea; *o*, auditory nerve; *p*, canal for carotid artery; *q*, part of glenoid fossa; *r*, styloid process.

by holding the breath, and forcing air from the throat into the Eustachian tube, so as to make the membrane bulge-out by pressure from within; or by exhausting the cavity by an effort at inspiration, with the mouth and nostrils closed, which will cause the membrane to be pressed inwards by the external air. In either case, the hearing is immediately found to be imperfect; but the deficiency relates only to grave sounds, acute ones being heard even more plainly than before. There is a different limit to the acuteness of the sounds of which the ear can naturally take cognizance, in different persons. If the sound be so high in pitch, that the membrana tympani cannot vibrate in unison with it, the individual will not hear it, although it may be loud; and it has been noticed, that certain individuals cannot hear the very shrill tones produced by particular Insects, or even Birds, which are distinctly audible to others.

715. The vibrations thus transmitted to the membrane covering the fenestra ovalis, will act upon the fluid contained within the labyrinth, which consists of the 'vestibule' (Fig. 291, *l*), the semicircular canals (*m*), and the cochlea (*n*). The vestibule is evidently the part that corresponds with the simple cavity, which constitutes the entire organ of hearing in the lower animals; and the others may be regarded as extensions of it for particular purposes.—In all Vertebrata save the lowest Fishes, three *semicircular canals* exist; and they uniformly lie in three different planes, at right angles to each other, corresponding to the bottom and two adjoining sides of a cube; hence it has been supposed, and with much apparent probability, that they assist in producing the idea of the *direction* of sounds. The form of the *cochlea* is nearly that of a snail-shell, being a spiral canal, excavated in the solid bone, and making about two turns and a-half round a central pillar; this canal, however, is divided into two by a partition which runs along its entire length, and which is formed partly by a thin lamina of bone, and partly by a delicate membrane. The two passages do not communicate with each other, except at the summit of the helix; and at their lower end they terminate differently, one opening freely into the vestibule, and the other communicating with the cavity of the tympanum, by an aperture termed the 'fenestra rotunda,' which is closed by a membrane.—These cavities are lined by a membrane, on which the ramifications of the auditory nerve (*o*) are minutely distributed, and in which may be found cells that appear to be nerve-vesicles; and the distribution of this nerve is peculiarly close and abundant on the 'lamina spiralis' of the cochlea. Hence the nerve will be affected by the sonorous undulations into which the included fluid is thrown; and these will probably be rendered more free than they are in those forms of the auditory cavity in which it is completely enclosed within bony walls, by the existence of the second orifice leading from the cochlea to the tympanic cavity. The cochlea has been supposed to be the organ which enables us to judge of the *pitch* of sounds; an idea that derives some confirmation from the correspondence between the development of the cochlea in different animals, and the variety in the pitch (or length of the scale) of the sounds which it is important that they should hear distinctly, especially the voices of their own kind.—A pair of 'otolithes,' formed of particles of carbonate and phosphate of lime cemented-together by animal mucus, is found in the vestibular sac.

716. The history of the development of the Auditory organ in the higher Vertebrata, presents a series of facts of great interest, of which the following is an outline.—The apparatus takes its origin in a portion of the Epencephalic vesicle, or 'vesicle of the medulla oblongata' (Fig. 262, B, *k*), which protrudes on either side, its cavity at first communicating with that of the vesicle, which remains permanent as the 'fourth ventricle.' As its protrusion increases, it becomes elongated and pear-shaped, and is only connected with the central mass by a pedicle whose canal gradually closes-up; the sac thus cut-off becomes the vestibular cavity, and the pedicle the auditory nerve. At first there is no vestige either of cochlea, semicircular canals, or tympanic apparatus; but the sac presents the simple character which it permanently retains in the Cephalopoda and the lower Fishes. Gradually, however, the semicircular canals are developed, by a contraction and folding-in of the walls of the vestibular sac; and the cochlea is probably formed as an offset from it. At the same time, the formation of cartilage, and subsequently of bone, takes place around the auditory sac and its prolongations, forming the 'sense-capsule,' which, in the higher Vertebrata, coalesces with the vertebral elements to form the temporal bone.—It is very interesting to remark, that the membranous labyrinth, between the eighth and thirteenth days in the Chick, has a structure almost precisely similar to that of the retinal expansion of the same period; consisting, like it, of a distinct but very delicate fibrous mesh-work, in the spaces between which are deposited a quantity of granular matter and numerous nucleated cells, whilst its exterior is composed of a dense mass of nuclei, almost precisely analogous to the granular particles which form a large part of the entire substance of the retina (§ 722).*

6. *Of the Sense of Sight.*

717. By the faculty of Sight, we are enabled to take cognizance of *luminous* impressions; and through these, we become acquainted with the form, size, colour, position, &c., of the objects that transmit or reflect light. But such knowledge can only be acquired (so far, at least, as we have the means of judging) through the medium of an optical instrument, which shall form upon the expanded surface of the Optic nerve an exact picture of surrounding objects, resembling that which is formed by the Camera Obscura; and it is from the conveyance of the impression produced by this picture to the Sensorium, that we derive the consciousness of that impression, on which we base our notion of the object which has produced it. This optical instrument, or Eye, may exist, as we shall presently see, under a great variety of conditions; but it will be only when it is sufficiently perfect to form a distinct picture, that any definite knowledge of surrounding objects can be obtained through its means. There are, however, in many of the lower animals, certain coloured spots, which, from their position, nervous connections, and resemblance to the lowest forms of undoubted visual organs, must be regarded as rudimentary eyes; but all the information to which we can suppose these to be subservient, will be the reception of vague impressions of light and darkness.—The lowest animals in which any such organs

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* See Mr. H. Gray, in "Philosophical Transactions," 1850.

have been distinguished,[*] are the *Echinodermata;* ocelliform spots having been observed by Prof. E. Forbes at the extremities of the rays of certain *Asteriada,* where they are connected with the extremities of nerve-filaments, and are protected by a peculiar arrangement of minute spines around each; and also by Ehrenberg on the surface of each of the five plates that alternate with the genital plates around the anal orifice of *Echinida.* Among the lower *Articulata,* the development of the visual apparatus does not seem to pass this rudimentary grade. In the animals belonging to the class of *Entozoa,* no distinct trace of visual organs has been detected; though among the *Planariæ* and other *Turbellaria* which range freely in search of their food, there are, as in *Leeches,* numerous eye-spots disposed about the head, by which it may be supposed that their movements are in some degree guided. Similar eye-spots may be seen upon the cephalic projection of the *Rotifera* (Fig. 96, *b*); and they become much more distinct in the *Annelida* (especially those of the *Dorsibranchiate* order), among which the rudiments of a proper optical instrument begin to show themselves, although these are sometimes buried beneath the integuments. It is singular that in certain of the last-named animals, eyes exactly resembling those elsewhere found on the *head,* should present themselves on the extremity of the *tail,* whose movements they obviously seem to direct.[†]—The same may be said of the lower Mollusca. Ocelliform spots have been observed in the neighbourhood of each orifice of several *Tunicata;* and numerous eyes may be distinguished along the margin of the mantle of *Pecten* and several other *Conchifera*—each of them having a sclerotic coat, with a cornea in front; a coloured iris, with its pupil, continuous with a layer of pigment lining the sclerotic; a crystalline lens and vitreous body; and a retinal expansion, proceeding from an optic nerve which passes from these bodies to the circum-palleal trunk (§ 642).[‡]

718. The Eyes of most of the higher *Articulated* animals, are constructed upon the *composite* type; each of the masses that is situated upon either side of the head, being made-up of an aggregation of single eyes, every one of which is in itself a complete visual instrument, but is adapted to receive and to bring to a focus those rays only which come to it in one particular direction. In most *Insects,* each composite eye forms a large hemispherical protuberance, which occupies a considerable part of the side of the head (Fig. 292); and when examined with a microscope, its surface is seen to be divided into a vast number of facets, which are usually hexagonal. The number of these facets, every one of which is the 'cornea' of a distinct eye, is usually very great; in the common House-fly there are about 4000; in the Cabbage Butterfly, 17,000; in the Dragon-fly, 24,000, and in the Mordella-beetle, 25,000. Behind the cornea is a layer of dark pigment, which takes the place and serves the purpose of the 'iris' in the eyes of Vertebrata; and this is perforated by

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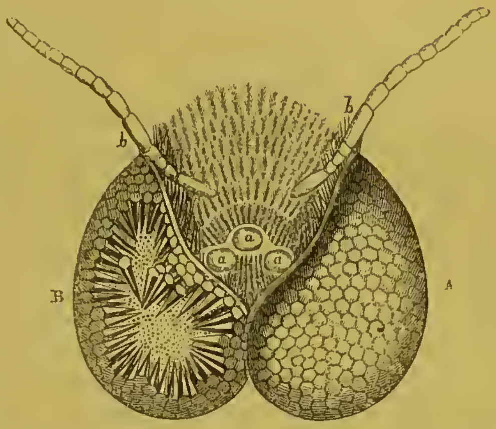
[*] No account is here taken of the red spots seen in many *Animalcules,* since there is not the least reason for believing them to be ocelli, similar spots having been seen in many undoubtedly-Vegetable cells; and the supposed ocelli at the margin of the disk of *Medusæ* are more probably auditory vesicles (§ 711). It is by no means unlikely, however, that rudimentary ocelli do exist in that class.

[†] See M. de Quatrefages, in "Ann. des Sci. Nat.," 3e Sér., Zool., Tom. XIII.

[‡] These bodies, previously noticed by Poli, Garner, and other Malacologists, have been minutely described by Will ("Froriep's Neue Notizen," 1844, Nos. 622 and 623).

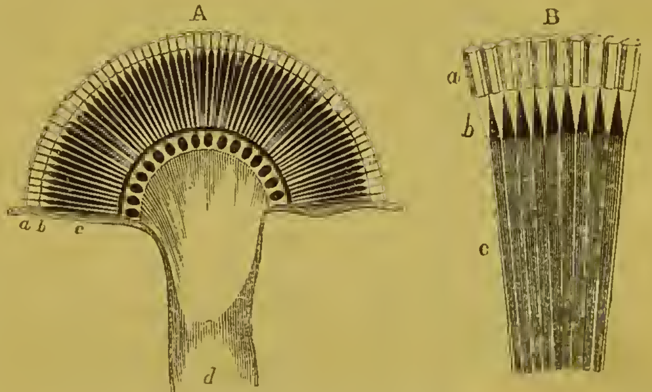
a central aperture or 'pupil,' through which the rays of light that have traversed the cornea, gain access to the interior of the eye. When a vertical section is made of one of these composite eyes, it is seen that each separate ocellus is the frustrum of a pyramid, of which the cornea forms the large end, or base (Fig. 293, *a*), whilst the small end abuts upon a bulbous expansion of the optic nerve; the interior of this pyramid is occupied by a transparent substance (*b*), which represents the 'vitreous humour:' and the pyramids are separated from each other by a layer of dark pigment, which completely encloses them, save at the pupillary apertures, and also at a corresponding set of apertures at their smaller ends, where the pigment is perforated by the fibres of the optic nerve (*c*), of which one proceeds to each separate eye. Each facet, or 'corneule,' of the common cornea, is usually convex on both its surfaces; and thus acts as a lens, the focus of which has been ascertained by experiment to be equivalent to the length of the transparent pyramid behind it; so that the image produced by the lens will fall upon the extremity of the filament of the optic nerve which passes to its truncated end. The rays which have passed through the several 'corneules' are prevented from mixing with each other, by means of the layer of black pigment which surrounds each cone; and thus no rays, except those which correspond with the axis of the cone, can reach the fibres of the optic nerve. Hence it is evident that each separate eye must have an extremely limited range of vision; being adapted to receive but a very small pencil of rays proceeding from a single point in any object; and as these eyes are usually immovable, they would afford but very imperfect information of the position of surrounding objects, were it not for their enormous multiplication, by which a separate eye is provided (so to speak) for each point to be viewed. No two of the

Fig. 292.



Head and Compound Eyes of the *Bee*, showing the ocelli *in situ* on one side (A), and displaced on the other (B); *a, a, a*, stemmata; *b, b*, antennæ.

Fig. 293.

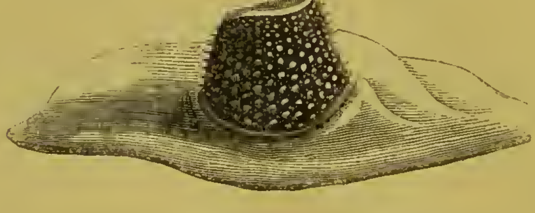


A, Section of the eye of *Melolontha vulgaris* (Cockchaffer): B, a portion more highly magnified:—*a*, facets of the cornea; *b*, transparent pyramids surrounded with pigment; *c*, fibres of the optic nerve; *d*, trunk of the optic nerve.

separate eyes, save those upon the opposite sides of the head which are directed exactly forwards, can form an image of the same point at the same time; but the combined action of all of them may give to the Insect, it may be imagined, as distinct a picture as that which *we* obtain by a very different organisation. At any rate, it seems certain, from observation of the movements of Insects, that the vision by which they are guided must be very perfect and acute.—Although the foregoing may be considered the typical structure of the eyes of Insects, yet there are various slight departures from it in the different subdivisions of the class. Thus in some cases, the posterior surface of each 'corneule' is concave, and a space is left between it and the iris, which seems to be occupied by a watery fluid or 'aqueous humour;' in other instances, again, this space is occupied by a double-convex body, which seems to represent the 'crystalline lens;' and there are cases in which this 'crystalline lens' is found behind the iris, the number of eyes being reduced, and each individual eye being larger, so that the entire aggregate approaches, both in its structure and its mode of action, to that of Arachnida and certain Crustacea.—Besides their composite eyes, Insects usually possess a small number of rudimentary single eyes, resembling those of the Arachnida; these are seated upon the top of the head, and are called *stemmata* (Fig. 292, *b*). Their precise use is unknown; but that they have considerable influence on the direction of the movements, appears from the fact, that if the stemmata of a Bee be covered with paint, it will fly continually upwards on being let go,—a fact which seems related to those already mentioned, in regard to the influence of visual sensations upon automatic movements (§ 679). It is remarkable that the larvæ of Insects which undergo a 'complete' metamorphosis, only possess simple eyes; the composite eyes being developed, at the same time with the wings and other parts which are characteristic of the Imago state, during the latter part of the Pupa condition.

719. In the higher *Crustacea*, the structure of the Eyes is nearly the same as in Insects; but the compound masses are not so large relatively to the bulk of the body, and the number of distinct eyes is not nearly so great. The facetted cornea which covers the aggregation of *ocelli*, is continuous with the external integument of these animals, and is thrown-off at each exuviation, a new one being previously formed beneath it. In some of the Entomostracous Crustacea, the compound eyes are formed upon the same plan, but differ in the smoothness of the surface of the cornea; in others, however, as in Myriapoda, each aggregate mass is composed of a small number of 'simple' eyes, of which every one has its own separate cornea, as well as its own crystalline lens and vitreous humour; and these in some instances are altogether detached from each other, whilst in other cases

FIG. 294.



Facetted eye of *Asaphus caudatus*.

they are fused into a single mass. It is peculiarly interesting to find the facetted surface of the eyes (Fig. 294) extremely well marked in the fossil remains of the extinct *Trilobites* (Fig. 76, A); this character alone having been sufficient to stamp them as Articulated animals, and to indicate their general position in the series.* Among some of the *Suctorial Crustacea*, the visual organs are altogether wanting in their state of full development, although they are uniformly present in their early condition. The same has usually been believed of the *Cirrhipeds;* but from the recent researches of Leidy and Darwin, it appears that eyes may be detected in the adults of many species, both sessile and pedunculated. Each compound mass consists of eight or ten lenses, enclosed in a common membranous bag or cornea, but surrounded by their separate envelopes of pigment; and the masses belonging to the two sides of the body are approximated on the median plane, and are sometimes fused together into one. The eyes are always situated deep within the body, so that the rays of light cannot reach them without passing through a considerable amount of superjacent tissue; and all that they seem adapted to communicate, is the impression made by light or darkness.†

720. Among *Arachnida,* which in this as in many other respects present an approximation to Vertebrata, we find a great reduction in the number of eyes, which are never more than eight in number (sometimes being only two), and are to be compared with the 'stemmata' of Insects, rather than with their compound eyes. These eyes are sometimes collected into one mass on the summit of the cephalo-thorax (Fig. 279, *c*), and are sometimes disposed symmetrically and separately on the two sides of the median line. In the Scorpions, we find two large eyes placed on the dorsal aspect of the cephalo-thorax, near the median line; and three pairs of smaller ones, which are placed on the outer margins of the same division of the body. The larger eyes are described by Müller‡ as each possessing a 'cornea,' which is convex anteriorly and concave posteriorly; and a nearly globular 'crystalline lens,' resembling that of Fishes, whose anterior surface lies in the hollow of the cornea, while its posterior rests upon the 'vitreous humour' without being imbedded in it. The 'vitreous humour' is a nearly hemispherical mass of soft granular matter, being almost flat in front, and very convex behind; over its posterior surface is spread the 'retina,' or expansion of the optic nerve; and this is covered by a thick layer of pigment, which passes inwards in front of the vitreous humour, so as to form a sort of iris, the pupillary aperture of which, however, exceeds the diameter of the crystalline lens.

721. Among those classes which constitute the higher division of the *Molluscous* series, in virtue of the possession of a distinct 'head,' the presence of visual organs is by no means constant; many Gasteropoda and Pteropoda being destitute of them altogether, and others only possessing ocelliform spots, which may be concluded to be rudimentary eyes, from

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* It is maintained by Burmeister ("The Organization of Trilobites," translated and published for the Ray Society, pp. 18, 19), that the common cornea of the composite eyes of these animals was always smooth, as it is in *Branchipus* and many other existing Entomostraca; and that the facetted surface is produced by the loss of the smooth cornea by decomposition.

† See Mr. Darwin's "Monograph on the Cirripedia," pp. 49—51.

‡ "Vergleichenden Physiologie des Gesichtsinnes," and "Ann. des Sci. Nat.," Tom. XVII.

their similarity in position to the eyes of those which undoubtedly possess visual powers. Even when most developed, the eyes are generally very minute in proportion to the bulk of the body, and in no instance do they present a high type of structure; their general organisation, indeed, bears a close resemblance to that which has been described in the eye of the Scorpion. In the *Cephalopoda,* however, we find the visual organs presenting a much larger size, and attaining a much higher grade of development; in accordance with the greater functional activity required in directing the rapid and energetic movements practised by a large proportion of these animals. We here find nearly all the principal parts, which are characteristic of the eye of higher animals; namely, a cornea, an anterior chamber filled with an aqueous fluid enclosed in a distinct capsule, a crystalline lens of globular form (as in Fishes), a large posterior chamber filled with vitreous humour, a tough fibrous or 'sclerotic' coat, a vascular 'choroid' coat within this, covered by black pigment upon its inner surface, and a retinal expansion. The relations of this last to the optic ganglion, however, are very peculiar. This ganglion is situated almost close to the back of the eye; and instead of transmitting a single optic nerve, as in higher animals, it gives-off a multitude of filaments, which separately pierce the sclerotic coat, and then form a plexus between this and the choroid, which has been mistaken for the retina.* The true retina, however, is a very thin lamella, apparently composed of vesicular nerve-substance, which is found between the pigment and the membrane inclosing the vitreous humour, and which communicates with the net-work of nerve-tubes on the outside of the pigmentary layer, by filaments passing through the latter. No proper 'iris' exists in the eyes of Cephalopoda; but its place is supplied by a partial prolongation of the sclerotic coat over the front of the crystalline, a central pupillary aperture being left. The cornea is not, like the true cornea of higher animals, a transparent continuation of the sclerotic coat, but is a modification of the general integument, analogous rather to the external or conjunctival layer of the cornea of Vertebrata; it is remarkable that in some Cephalopoda, it should be perforated by an orifice of considerable size, through which the capsule of the crystalline lens projects into the external medium.†

722. There are but few exceptions to the general fact of the presence of distinct visual organs in the *Vertebrata;* and the type upon which these are formed, presents scarcely any essential diversity in the different classes (Fig. 295). In all we find the eye of nearly globular shape, with a projection in front caused by the greater curvature of the cornea. It is enclosed in a tough fibrous envelope, or 'sclerotic' coat (1), which supports the transparent 'cornea' (2); and this is lined by the vascular 'choroid' (3), of which the muscular 'iris' (6), that is interposed between the anterior and posterior chambers, may be regarded as in some sort a continuation. The choroid is lined by a layer of black pigment; and between this and the hyaloid membrane (or capsule of the vitreous humour) is interposed the 'retina' (8). The optic nerve, in all instances, is a

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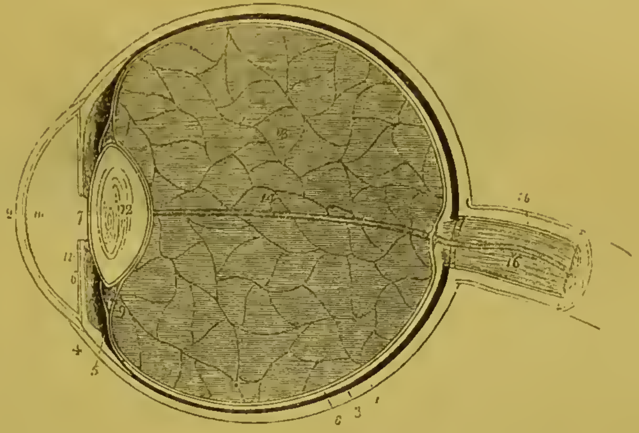
* The true nature and relations of this structure were first elucidated by Wharton Jones, in "Lond. and Edinb. Phil. Mag.," 3rd Ser., Vol. VIII. (1836); see also Power in "Dublin Journ. of Med. Sci., Vol. XXII. (1842).

† The homologies of this aberrant structure are very differently interpreted by different Anatomists. See Siebold's "Vergleichende Anatomie," § 247.

single trunk, which perforates the sclerotic and choroid coats at the back of the eye, and then spreads-out into a fibrous network, which is covered on its free surface by a layer of vesicular or ganglionic matter. It is of this, indeed, that the nervous portion of the retina is chiefly composed; and the nerve-vesicles here found can scarcely be distinguished from those of the grey matter of the brain. This is, perhaps, the best example we possess, of the general doctrine, that the changes commencing at the peripheral extremities of the afferent nerves, are probably effected by the agency of cells, like those which originate at the central origins of the efferent.

Fig. 295.



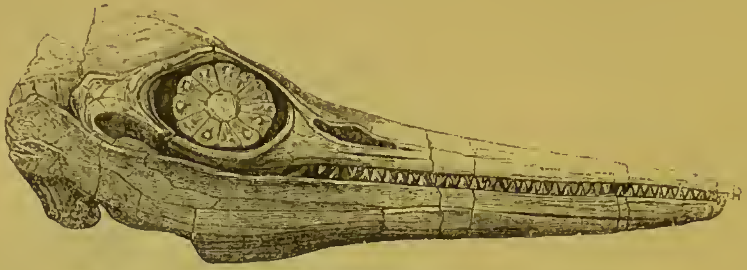
Longitudinal section of the globe of the *Human Eye:*—1. The sclerotic, thicker behind than in front. 2. The cornea, received within the anterior margin of the sclerotic, and connected with it by means of a bevelled edge. 3. The choroid, connected anteriorly with (4) the ciliary muscle, and (5) the ciliary processes 6. The iris. 7. The pupil. 8. The retina, or expansion of the optic nerve, terminating anteriorly by an abrupt border at the commencement of the ciliary processes. 9. The canal of Petit, which encircles the lens (12); the thin layer in front of this canal is the zonula ciliaris, a prolongation of the vascular layer of the retina to the lens. 10. The anterior chamber of the eye, containing the aqueous humour: the lining membrane by which the humour is secreted is represented in the diagram. 11. The posterior chamber. 12. The lens, more convex behind than before, and enclosed in its proper capsule. 13. The vitreous humour enclosed in the hyaloid membrane, and in cells formed in its interior by that membrane. 14. A tubular sheath of the hyaloid membrane, which serves for the passage of the artery of the capsule of the lens. 15. The neurilemma of the optic nerve. 16. The arteria centralis retinæ, embedded in the centre of the optic nerve.

The refractive media contained in the interior of the eye are always three in number, and of different densities; the anterior chamber (10) being occupied by the 'aqueous humour,' which is a limpid watery fluid; the 'crystalline lens' (12), a substance of considerable firmness, whose convexity is much less in the terrestrial than in the aquatic Vertebrata, being placed immediately behind the iris; and the great bulk of the posterior chamber being occupied by the 'vitreous humour' (13), which is of the consistence of thin jelly.

723. The eye of *Fishes* is chiefly remarkable for the great density and spherical form of the crystalline lens, which enable it to exert the necessary refracting influence upon rays which come to the organ through water; and also for the presence of the body termed the 'choroid gland,' a vascular erectile organ at the back of the eye-ball, which, like the 'pecten' in the eye of the Bird, may be concerned in the adaptation of the eye to distinct vision at different distances.—The eye of *Reptiles* presents no remarkable peculiarity; except in the rudimental existence, among certain Chelonia and Sauria, of that osseous capsule which is so largely developed in the extinct Enaliosauria (Fig. 296), and which performs a most important office in the eyes of Birds. We here first meet, however, with a special arrangement of the integuments of the face for the protection of this delicate organ; for whilst in Serpents the skin of the head passes

continuously in front of the eyes, merely becoming transparent where it covers the cornea, it is doubled in most other Reptiles into two folds, constituting the upper and lower eyelids, which can be drawn-together by a sphincter muscle; and we also find a rudiment of the third eyelid, formed by an additional fold of membrane at the inner angle, which is fully developed in the Batrachia and in the Crocodile, into a 'nictitating membrane' resembling that of Birds.—The eye of *Birds* is generally large; and it is obvious from the habits of these animals, that their visual power is extraordinarily acute. The tough fibrous investment of the globe is very commonly strengthened in front by a circle of bony plates, usually from twelve to fifteen in number; and among other purposes which these plates appear to serve, is that of giving a fixed point of action to the special muscular apparatus, by which the adaptation of the eye to varying distances is effected. The eye of Birds is also remarkable for the presence of a peculiar body, termed the *pecten* or *marsupium*, which projects-forwards from the fissure of entrance of the optic nerve into the vitreous humour; it is chiefly composed of a layer of blood-vessels, constituting an erectile tissue, folded in numerous plications, the size, form, and number of which vary considerably in different Birds, even such as are otherwise closely allied; and the whole is covered by a continuation of the black pigment which lines the choroid. The uses of this organ are not certainly known; it may, perhaps, serve more than one purpose; but its action seems not improbably to be connected with the adaptation of the eye to distances, the relative positions of the crystalline lens and the retina being altered when its vessels are distended with blood. The third eyelid or 'nictitating membrane' here attains its highest development, being drawn rapidly and frequently across the eye by a special muscular apparatus, for the purpose of sweeping impurities from its surface, whilst, being translucent, it does not offer any great impediment to the admission of light.—The general plan of structure of the Eye in *Mammalia* does not depart much from the type of the organ in Man; though there are several minor variations in different orders. Thus in Cetacea, the crystalline lens is nearly globular, as in Fishes; and in most Quadrupeds, a portion of the choroid is lined with a pigment-layer of metallic lustre, called the *tapetum*, which is silvery in the Carnivora, and blue-green in the Herbivora. In the Ornithorhyncus alone do we find a circlet of bony plates in the sclerotic coat. The visual power of Mammals appears on the whole to be inferior to that of Birds, especially in the power of accommodation to a range of distance.

Fig. 296.

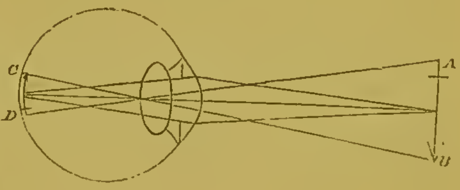


Skull of *Ichthyosaurus*, showing the osseous sclerotic plates.

724. The development of the Eye in the higher Vertebrata commences by a protrusion from a part of the Deutencephalic portion of the brain, or 'vesicle of the thalami optici' (§ 679), which is at that time hollow; and the cavity of the protrusion is continuous with that of the vesicle itself, which remains as the 'third ventricle.' The protrusion is lined, like the vesicle itself, with granular matter, which gradually becomes distinctly cellular, forming a layer of truly ganglionic character; and whilst this change is taking place, the protrusion increases, becomes pear-shaped, and is at last connected only by a narrow pedicle with the vesicle from which it sprang. This pedicle closes-up, so as completely to separate the two cavities; and the one which has been thus budded-forth constitutes the rudiment of the eye, whilst the other goes on to form the ganglionic bodies at the base of the cerebrum, and the connecting pedicle becomes the optic nerve, which connects the retina with its ganglionic centre. The spherical extremity of the protrusion is absorbed, and the retina, or vesicular lining, becomes attached to the margin of the lens, which is in the mean time developed in the interior of the cavity, and is at first completely surrounded by the retina. The formation of the coats of the Eye takes place subsequently; the development even of the 'fibrous lamina' and of the 'membrana Jacobi' of the retina itself, not taking place until after its cellular layer has been very distinctly formed.*—It is a curious circumstance, and one not very easy to account-for, that the development of the Eye should take place from the Deutencephalic and not from the Mesencephalic vesicle; as it is in the latter that the proper 'optic ganglia' originate, with which the optic nerves come at last to have their principal connection, their connection with the 'thalami optici' being much less close.

725. In the most perfect form of the Eye, such as that presented by Vertebrata generally, the luminous rays which diverge from the several points of any object, and fall upon the front of the cornea, are refracted by its convex surface, whilst passing through it into the eye, and are made to converge slightly. They are brought more closely together by the crystalline lens, which they reach after passing through the pupil; and its refracting influence, together with that produced by the vitreous humour, is such as to cause the rays that issued from each point, to meet in a focus on the retina. In this manner, a complete inverted image is formed, as shown in Fig. 297, which represents a vertical section of the eye, and the general course of the rays in its interior; those which issue from the point A being brought to a focus at D, whilst those diverging from B are made to converge upon the retina at C. The retina, which is itself so thin as to be nearly transparent, is spread over the layer of black pigment, which lines the choroid coat. The purpose of this is evidently to *absorb* the rays of light that form the picture, immediately after they have passed through the retina; in this manner, they are prevented from being reflected from one part of

Fig. 297.



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* See Mr. H. Gray in "Philosophical Transactions," 1850.

the interior of the globe to another, which would cause great confusion and indistinctness in the picture. Hence it is that in those *albino* individuals (both of the Human race, and among the lower animals), in whose eyes this pigment is deficient, vision is extremely imperfect, except in a very feeble light; for the vascularity of the choroid and iris is such, as to give to these membranes a bright red hue, which enables them powerfully to reflect the light that reaches the interior of the eye, when they are not prevented from doing so by the interposition of the pigmentary layer.—The Eye is so constructed, as to avoid certain errors and defects, to which all ordinary optical instruments are liable. One of these imperfections, termed *spherical aberration,* results from the fact, that the rays of light, passing through a convex lens whose curvature is circular, are *not all* brought to their proper foci; those which have passed through the exterior of the lens, being made to converge sooner than those which have traversed its central portion. The result of this imperfection is, that the image is deficient in clearness, unless only the central part of the lens be employed.—The other source of imperfection is what is termed *chromatic aberration;* and it results from the unequal degree in which the differently-coloured rays are refracted, so that they are brought to a focus at different points. The violet rays, being the most refrangible, are soonest brought to a focus; and the red, being the least refrangible, have their focus at the greatest distance from the lens. Hence it is impossible to obtain an image by an ordinary lens, in which the colours of the object are accurately represented; for the foci of its differently-coloured portions will be different; and its white rays will be decomposed, so that the outlines will be surrounded by coloured fringes.—The Optician is enabled to correct the effects of these aberrations, by combining lenses of different densities and curvatures; so arranged as to cover each other's errors, without neutralizing the refractive power. This is precisely the plan adopted in the construction of the Eye; which, when perfectly formed, and in a healthy state, forms an accurate picture of the object upon the retina, free from either spherical or chromatic aberration. This is effected by the combination of *humours* of different densities, having curvatures precisely adapted to the required purpose.

726. The power, by which a healthy well-formed Eye can accommodate itself to the distinct vision of objects at varying distances, is a very remarkable one; and its rationale is not yet perfectly understood. According to the laws of Optics, the picture of a near object can only be distinct, when formed more remotely from the lens than the picture of a distant object. Consequently when the eye, that has been looking at a distant object, and has seen it clearly, is turned to a near object, a distinct picture of the latter cannot be formed, without some alteration in the distance either of the cornea or of the lens from the retina, or in the curvature of their refracting surfaces. It seems most probable that the adjustment is chiefly effected by the 'ciliary muscle,' which is a collection of muscular fibres, radiating from the junction of the cornea and sclerotic, to the 'ciliary processes' of the choroid, which hold the lens in its place; for by the contraction of this muscle, the lens will be drawn forwards, and the eye thus adapted for the vision of near objects. In the Human eye, the ciliary muscle consists of 'non-striated' fibres; but in the eyes of

Birds, in which it is much more highly developed, it is formed of 'striated' fibres; whilst, by the partial ossification of the anterior portion of the sclerotic coat, its origin is more securely fixed.* It does not seem improbable that the 'pecten' or peculiar erectile organ in the vitreous humour of the Bird's eye (§ 723), may be subservient to this adjustment; for, when the lens is carried forwards, a vacuity must exist behind it, which the entrance of blood into this plexus of vessels will supply. It seems quite certain, from observation of the actions of Birds, that they must possess the power of adapting their eyes to distinct vision at different distances, in a higher degree than any other animals. The 'choroid gland' of the Fish's eye (§ 723) may not improbably answer a similar purpose.—The adjustment is probably in all cases, as in Man, a purely 'automatic' action, taking place without any voluntary effort, whenever the visual sense is directed by the will to a special object; and it is a very good example of that class of actions, in which *sensation* is a necessary link in the chain of reflex action (§ 678).

727. Another automatic action, which adapts the eye for distinct vision under varying degrees of light, is the alteration in the diameter of the 'pupil.' This is effected by the muscular structure of the 'iris,' which is made-up in many animals (though not distinctly so in Man) of two sets of fibres, a circular and a radiating; the aperture of the pupil being diminished by the contraction of the former, when the light is powerful, so as to exclude its excess from the interior of the eye; and being augmented by the contraction of the latter, when the light is faint, so as to admit the greatest possible number of rays. The contraction of the pupil also takes place when vision is directed to any very near object; and its purpose appears then to be, to prevent the rays from entering the eye at such a wide angle, as would render it impossible for them to be all brought to their proper foci, and would thus produce an indistinct image. In either case, the regulation of the diameter of the pupil is an action with which the will has nothing to do, and which it cannot execute by any direct effort.—It is worthy of note, that in Birds the fibres of the iris are very strongly marked, and that they are of the 'striated' kind. The diameter of the pupil is often seen to vary in them, without any change in the amount of light, or any alteration in the position of the eyes, whence it has been supposed that they possess a voluntary power over this movement; but the fact is probably rather, that the alteration takes place in virtue of a change in the direction of the sight from a near to a distant object, or *vice versâ*, which may occur without any obvious difference in the position of the eyes, when the two objects are in the same line, and the eyes are placed at the sides of the head, and not in front,—as in the Parrot, in which this change has been most frequently observed. When the eyes are so situated that both of them can be directed to the same object, their axes are made to converge in it; and the angle at which they meet, which will be very acute when the object is distant, increases rapidly as the object is approximated to the eyes. It is from the 'muscular sense,' which informs us of the condition of the muscles thus brought into conjoint action, that we derive our chief information as to the *distance* of objects, by an instinctive inter-

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* See Messrs. Todd and Bowman's "Physiological Anatomy and Physiology of Man," Vol. II., p. 27.

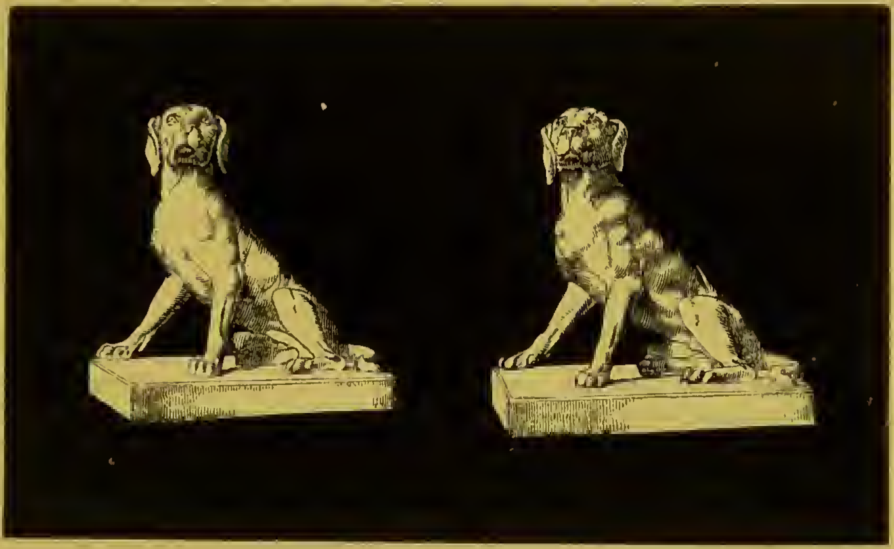
pretation of the impressions thus made upon our consciousness. It is quite certain that in Man, this instinctive apprehension is *acquired;* for the infant, or a person who has newly become possessed of vision, is only able to form it after a long course of experimental training. It is equally certain, on the other hand, that in many of the lower animals it must be *congenital;* since they perform actions, which manifest a power of accurately estimating distances, and of regulating their muscular movements accordingly, immediately on their entrance into the world (§ 701).

728. A considerable variety exists among Vertebrated animals, in regard to the position of the Eyes, and the degree in which they possess the same range of vision. It would seem as if a very extensive range of vision posteriorly, is necessary in such timorous animals as the Ruminants, which are almost always on the watch for enemies, and seek their safety in flight; that perfection of the visual sense, which (as will be presently shown) can only be gained by the combined use of the two eyes, being sacrificed in them to the power of seeing round the whole horizon at once, which they possess in virtue of the lateral position of their eyes. Where the position of the eyes is such, that their spheres of vision are entirely distinct (as happens in many Fishes), the optic nerve proceeding from each eye passes direct to the ganglion on the opposite side; but where, as most commonly happens, the range of one eye overlaps (so to speak) that of the other, so that both see the same object at once, if it be within that overlapping portion, a different arrangement of the fibres of the optic nerves prevails; for those of such parts of the retinæ of both eyes, as look towards the same side (*i. e.* the inner portion of the retina of the right eye, and the outer portion of the retina of the left, and *vice versâ*), pass to the ganglion of the opposite side; so that each eye is connected with both ganglia. The effect, however, will still be the same; namely, to make each ganglion the seat of the visual impressions originating from sources on the opposite side of the body; and the purpose of this is probably, to bring the guiding sensations of sight into relation with the muscular movements they regulate. For, by a decussation of fibres in the Medulla Oblongata, the Sensory Ganglia above it are connected with *opposite* sides of the Spinal Cord below it; and thus, the sensations of visual objects on the *right* side of the body being derived through the *left* optic ganglion, their influence will be directly conveyed to the *right* side of the spinal cord, and to the muscles whose nerves originate from it.

729. Although the forward position of the eyes, by greatly diminishing the range of vision, might seem to detract from the advantage which is conferred by the possession of *two* eyes, yet it confers a great advantage of a different kind; for it is by the intuitive combination of the two *dissimilar* pictures, which are formed of any near object upon the retinæ of the two eyes, that we gain the impression of its projection or solidity. That the pictures *are* dissimilar, is easily shown by holding-up a thin book in such a manner that its back shall be in a line with the nose, and at a moderate distance from it; and the experimenter who looks at the book, first with one eye, and then with the other, will find that he gains a different view of the object with each eye, when used separately; so that if he were to represent it, as he actually sees it under these circumstances, he would have two perspective delineations differing from one another, because drawn from different points. But on looking at the

object with the two eyes conjointly, there is no confusion between these pictures; nor does the mind dwell upon either of them singly; but the mental union of the two intuitively gives us the idea of a solid *projecting* body,—such an idea as we could only have otherwise acquired by the exercise of the sense of touch. That this is really the case, has been proved by experiments with a very ingenious instrument, the Stereoscope, invented by Prof. Wheatstone; which is so contrived, as to bring to the two eyes, by reflection from mirrors, or refraction through prisms or lenses, two different pictures, such as would be accurate representations of a solid object, as seen by the two eyes respectively (Fig. 298). The images of these pictures being thrown on those parts of the two retinæ, which would have been occupied by the images of the solid (supposing *that* to have been before the eyes), the mind will perceive, not one or other of the single representations of the object, nor a confused union of the two, but a body projecting in *relief*, the exact counterpart of that from which the drawings were made.*—It is doubtless by a similar intuitive interpretation, that we recognize the erect position of objects, notwithstanding the inversion of their images upon our retinæ. This is certainly not a matter of experience; nor is it capable of explanation (as some have supposed) by a reference to the direction in which the rays fall upon the retina. It is the *Mind* which rectifies the inversion; and it is just as difficult to understand how the inverted image upon the retina should be taken-cognizance-of by the mind at all, as it is to comprehend how it should thus be rectified. In fact, there is no real connection whatever, between the inversion of the image upon the retina, and that wrong perception of external objects, which some have thought would be its necessary consequence.

Fig. 298.



Stereoscopic Figures.

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* The most wonderful reproduction, to the *mind's eye*, of the solid body, is effected when the two pictures employed are *photographic* representations, taken at the proper angular distance from each other.

CHAPTER XV.

OF THE SOUNDS PRODUCED BY ANIMALS.

730. The purposes of Animal existence frequently involve the necessity of such a communication between one individual and another, as can only be made by the production of Sounds on the one part, and by the Hearing of them on the other. The most general requirement of this kind, is probably that arising out of the Generative function, in those tribes in which the congress of two individuals is requisite; and we find that one or both of the sexes are often provided with the means of producing sounds, which indicate their presence to such of the opposite sex as may be within hearing of them. The sounds produced by Invertebrated animals are not vocal or articulate in their character, although they frequently serve to intimate the state of tranquillity or excitement of the individuals that utter them; and it is only in the higher Vertebrata, in which the apparatus of Voice is so constructed as to be capable of a great variety of actions, and is brought into relation with the respiratory organs, that it acquires its most expressive character. The restriction of articulate language to Man, is rather a result of the superiority of his *mental* than of his *vocal* endowments; since many Birds can execute a perfect imitation of the sounds which he utters, although incapable of attaining to more than a general comprehension of their import, and even this rather in the 'concrete,' than by the formation of any 'abstract' notions of the meaning of the separate words which they imitate.

731. Although certain of the *Nudibranchiate* Gasteropods have been occasionally heard to produce a clear bell-like sound, yet their mode of generating it is unknown; and they are the only animals of the Molluscous series, in which such an endowment has ever been observed.—It is among *Insects*, more than in any other class of Invertebrata, that the power of generating sounds is met-with. Some of these seem necessarily to arise during the ordinary movements of these animals; such is the 'hum' which is produced in flight, and which varies in its character from the dull droning sound of the common 'shard-borne beetle,' to the shrill trumpet of the gnat and mosquito, that serves to give warning of the proximity of these blood-thirsty insects. Generally speaking, the Insects that fly with the greatest force and rapidity, and with wings seemingly motionless (owing to the extreme rapidity of their vibrations), make the most noise; whilst those that fly gently and leisurely, and can be seen to fan the air with their wings (as is the case with most Lepidoptera), yield little or no sound. It appears, however, from the experiments of Burmeister, that in Bees and Flies, the sound is not so much produced by the simple motion of the wings, to which it is commonly attributed, as by the vibrations of a little membranous plate situated in each of the posterior spiracles of the thorax; for if the apertures of these be stopped, no sound is heard, even though the wings remain in movement. Other sounds are produced by the act of mastication; thus the noise occasioned by the armies of Locusts, when incalculable millions of

powerful jaws are in action at the same time, has been compared to the crackling of a flame of fire driven by the wind.—The sounds which are produced by special means, with direct reference to mutual communication, are generated in a great variety of modes. Thus, the neuters or 'soldiers' among the *Termites* make a vibratory sound, rather shriller and quicker than the ticking of a watch, by striking hard substances with their mandibles; and this seems to answer the purpose of keeping the 'labourers,' who answer it with a kind of hiss, alert and at their work. The well-known sound termed the 'death-watch,' is produced in a similar manner by the *Anobium*, a small beetle that burrows in old timber; if the signal be answered, it is continually repeated; whilst if no answer be returned, the animal changes its situation before again making its presence known. The noise exactly resembles that produced by tapping moderately with the nail upon the table; and the insect may often be brought to answer this imitation, as well as the real sound of its own kind. A very curious sound, the mode of whose production has not been certainly ascertained, is given-out by the *Sphinx atropos* (death's-head-moth), when confined or taken into the hand; this sound has been likened to the cry of a mouse, but is more plaintive and even lamentable. The peculiar 'hum' given off by *Bees* during their ordinary labours in the hive, is frequently so modified as to be (to all appearance) a means of communication between them; thus it assumes a sharp angry tone when the hive has been disturbed, especially if some of the bees have been killed; it is changed to a low and plaintive sound, when the queen has been taken away; and this is exchanged for a cheerful humming, which is speedily diffused through the entire community, when she is restored.—Of the sounds that seem especially to have reference to sexual communication, the most remarkable are those of the *Grasshopper*, and of the *Cicada* tribes. In the former, the sounds are produced by the attrition of the anterior pairs of wings against each other, one of the nervures being furnished with a rough file-like edge, which is made to pass over the nervures of the opposite wing; and the sound is augmented by the resonance of a certain part of the wing, that is surrounded by peculiarly strong nervures, between which the thin membrane is tightly stretched, so that it acts as a 'tympanum.' The sound-producing organs of the latter, however, are situated internally, and are somewhat complex in their structure. Their essential part seems to be a tense membrane, stretched across a cavity in the last segment of the thorax on either side, which is drawn-in or forced-out by the action of two opposing bundles of muscular fibres; and it is found that the sound is produced even in a dead specimen, when these muscles are pulled and suddenly let-go. Externally to this apparatus are other membranous plates, whose office appears to be to increase the sound by resonance; and so effectually do they act, that a certain Cicada of Brazil is said to be audible at the distance of a mile, which is as if a Man of ordinary stature possessed a voice that could be heard all over the world. The sound is often kept-up for some hours; resembling the 'hum' of Bees in its continuity, rather than the interrupted 'chirp' of Crickets.

732. Among *Vertebrata*, the production of Sounds appears to be confined to the air-breathing classes; no Fishes being known to possess the

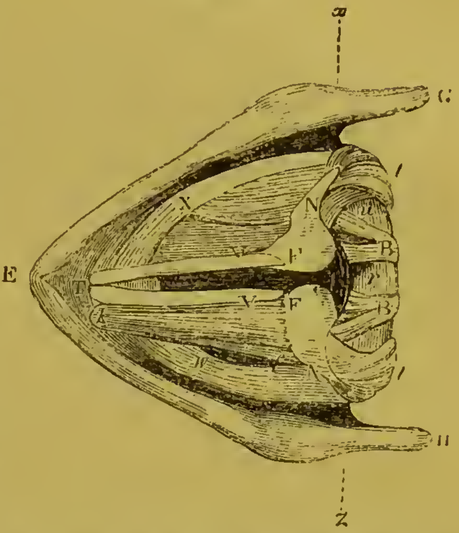
means of generating them.—In *Reptiles*, it is at the point where the trachea opens into the front of the pharynx, that the vibratory apparatus is situated, which gives-out sounds when air is forced through it from the lungs. The sounds produced by animals of this class, however, are of a very simple and inexpressive kind. Thus from Turtles, Serpents, and ordinary Lizards, we hear nothing else than a 'hiss,' occasioned by the passage of the air through the narrow fissure of the glottis; this sound being often much prolonged, owing to the great capacity of their lungs. In Frogs, a 'croak' is produced by the vibration of the lips of the glottis itself; and in the larger Crocodiles, Alligators, &c., this croak is augmented in its volume, and becomes a 'roar.' In these orders we find the rudiments of the proper 'larynx' of Mammals; which, however, are chiefly developed in the male sex.

733. In *Birds*, the situation of the vocal organ is very different. The summit of the trachea is furnished with a 'larynx,' provided with cartilages and muscles, in which many of the parts of the larynx of Man can be recognized; but the use of this seems to have reference entirely to the regulation of the ingress and egress of air. The vocal sounds for which Birds, as a class, are so remarkable, are formed by an organ which is altogether peculiar to them, and which is situated at the *lower* extremity of the trachea, just at its bifurcation into the bronchial tubes. The structure of this 'inferior larynx' varies greatly in different species, being most complex in those which are able to produce the greatest diversity of sounds; and in some Birds which are entirely voiceless (such as the Storks), the organ is entirely wanting. The two or three lowest rings of the trachea are usually consolidated into one; and in the interior of this, a cross-bone runs from front to back, which has a vertical semilunar membrane prolonged upwards from its upper edge. This seems analogous in its action to the vibrating tongues or plates of 'reed-instruments' of music; and it is put in motion by currents of air passing on either side of it. Each of the bronchial tubes has its own glottis for the regulation of the passage of air; and we also find a part of the walls of both the bronchial tubes and of the trachea, to be composed of a thin membrane, stretched tensely between cartilages, which serves as a 'tympanum,' to increase the loudness of the sounds by resonance. Sometimes we find special dilatations of the trachea, which are apparently subservient to the same purpose. The actions of the vocal apparatus are regulated in the Singing-birds by at least five pairs of muscles, besides those which increase or diminish the length of the trachea, a change which is of considerable importance in modifying the *pitch* of the notes. In those Birds which can imitate the articulate sounds of the Human voice, such as the Parrot, the Raven, and the Mocking-bird, the tongue is employed in their production.

734. In *Mammals*, one 'larynx' is made to answer the double purpose of regulating the ingress and egress of air, and of producing vocal tones. There are few, if any, of this class, which have not the power of producing some vocal sound; and the structure of their larynx generally corresponds pretty closely with that of Man, which will be briefly described as an example of the most complete form of vocal apparatus.—The Larynx is built-up, as it were, upon the *Cricoid* cartilage (Fig. 299, x *w r u*), which surmounts the trachea, and which might be considered as its highest ring,

modified in form, its depth from above downwards being much greater posteriorly than anteriorly. This is embraced, as it were, by the *Thyroid* cartilage (G E H); which is articulated to the sides of the cricoid by its lower horns, round the extremities of which it may be considered to rotate, as on a pivot. In this manner, the front of the thyroid cartilage may be lifted-up, or depressed, by the muscles which act upon it; whilst the position of its posterior part is but little changed. Upon the upper surface of the back of the cricoid cartilage, are seated the two small *Arytenoid* cartilages (N F); these are so tied to the cricoid by a bundle of strong ligaments (B B), as to have a sort of rotation upon an articulating surface, which enables them to be approximated or separated from each other, — their inner edges being nearly parallel in the first case, but slanting-away from each other in the second. To the summit of these cartilages are attached the *Chordæ Vocales*, or vocal ligaments (T U), composed of yellow fibrous or elastic tissue. These stretch-across to the front of the Thyroid cartilage; and it is upon their condition and relative situation, that the absence or the production of vocal tones, and all their modifications of pitch, depend. They are rendered tense by the depression of the front of the Thyroid cartilage, and relaxed by its elevation; by which action the *pitch* of the tones is regulated. But for the production of any vocal tones whatever, they must be brought into a nearly parallel condition, by the mutual approximation of the points of the arytenoid cartilages to which they are attached; whilst in the intervals of vocalization, these are separated, so that the *rima glottidis*, or fissure between the chordæ vocales, assumes the form of a narrow **V**, with its point directed backwards. Thus there are two sets of movements concerned in the act of vocalization;—the regulation of the relative position of the Vocal Cords, which is effected by the movements of the Arytenoid cartilages;—and the regulation of their tension, which is determined by the movements of the Thyroid cartilage. The Arytenoid cartilages are made to diverge from one another by means of the *Crico-arytenoidei postici* of the two sides (N *l*, N *l*), which proceed from their outer corners, and turn somewhat round the edge of the Cricoid, to be attached to the lower part of its back; their action is to draw the outer corners of the Arytenoid cartilages outwards and downwards, so that the points to which the vocal ligaments are attached are separated from one another, and the rima glottidis is thrown open. The action of these muscles is antagonised by that of the *Arytenoideus trans-*

Fig. 299.

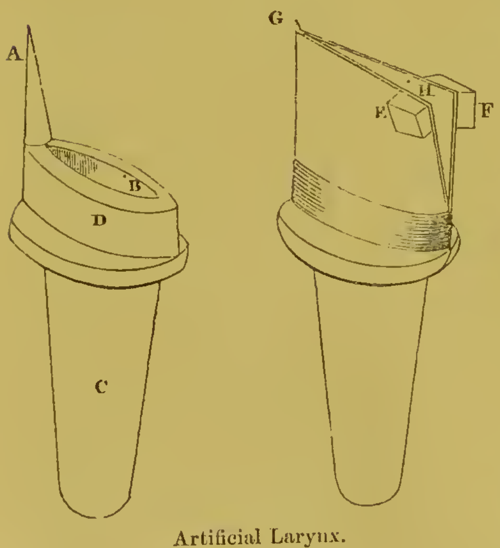


Bird's-eye view of *Human Larynx* from above:—G E H, the thyroid cartilage, embracing the ring of the cricoid X *w r u*, and turning upon the axis *x z*, which passes through the lower horns; N F, N F, the arytenoid cartilages, connected by the arytenoideus transversus; T V, T V, the vocal ligaments; N X, the right crico-arytenoideus lateralis (the left being removed); V *k f*, the left thyro-arytenoideus (the right being removed); N *l*, N *l*, the crico-arytenoidei postici; B B, the crico-arytenoid ligaments.

versus, which draws together the Arytenoid cartilages; and by that of the *Crico-arytenoidei laterales* of the two sides (N X), which run forwards and downwards from the outer corners of the Arytenoid cartilages, and tend by their contraction to bring together their anterior points, to which the Vocal ligaments are attached.—The depression of the front of the Thyroid cartilage, and the consequent tension of the vocal ligaments, are occasioned by the conjoint action of the *Crico-thyroidei* of the two sides, which occasions the Thyroid and Cricoid cartilages to rotate, the one upon the other, at the articulation formed by the inferior cornua of the former; and this action will be assisted by the *Sterno-thyroidei*, which tend to depress the front of the Thyroid cartilage, by pulling from a fixed point below. On the other hand, the elevation of the front of the Thyroid cartilage, and the relaxation of the Vocal ligaments, are effected by the contraction of the *Thyro-arytenoidei* of the two sides (V *k f*), whose attachments are the same as those of the Vocal ligaments themselves; and this is aided by the *Thyro-hyoidei*, which will tend to draw-up the front of the Thyroid cartilage, acting from a fixed point above.

735. During the ordinary acts of inspiration and expiration, the Chordæ Vocales appear to be widely separated from each other, and to be in a state of the freest possible relaxation. In order to produce a vocal sound, they must be made to approach one another, and their inner faces must be brought into parallelism; both of which ends are accomplished by the rotation of the Arytenoid cartilages: whilst, at the same time, they must be put into a certain degree of tension, by the depression of the Thyroid cartilage. Both of these movements take place consentaneously, and are mutually adapted to each other; the vocal ligaments being approximated, and the rima glottidis consequently narrowed, at the same time that their tension is increased.—It has been fully proved by the researches of Willis, Müller, and others, that the action of the Vocal ligaments, in the production of sound, bears no resemblance to that of vibrating strings; and that it is not comparable to that of the mouth-piece of the flute-pipes of the Organ; but that it is, in all essential particulars, the same with that of the 'reeds' of the Hautboy or Clarionet, or the 'tongues' of the Accordion or Concertina. An 'artificial larynx' has been constructed on this principle, which may be made to produce sounds very similar to the vocal tones of Man. Its general arrangement may be understood from Fig. 300; in which C is the pipe for the passage of air, D a ring at its summit for the attachment of the flexible vibrating plates, B its long and narrow orifice, A a pin that serves as a fixed point from which the tension may take place, whilst E, F are two bits of cork glued to the corners of the vibrating plates, by which they may be more conveniently moved and

Fig. 300.



Artificial Larynx.

strained, so as to bring the edges of the slit G H near-together and into parallelism, and to regulate their tension.—The loudness of the voice is often increased by some special apparatus of resonance. This is particularly the case with the 'Howling Monkeys' of America, whose larynx possesses several pouches opening from it, one of which is excavated in the substance of the hyoid bone itself. Although these Monkeys are of inconsiderable size, yet their voices are louder than the roaring of lions; that of a single individual is distinctly audible at a distance of two miles; and when a number of them are congregated together, the effect is terrific.

736. The actions of the Larynx are among the most interesting examples of the use made by Volition of the automatic portion of the nervous apparatus (§ 693). For the Will cannot influence the state of contraction of any of the vocalizing muscles, *except in the act of vocalization*; and it is requisite for the performance of this act, that the tone to be produced should have been previously conceived (however momentarily) in the mind, so that this conception takes the place of the guiding sensation, in regulating the actions of the muscles which produce it (§ 683). When this cannot be formed, in consequence of congenital absence of the sense of hearing, the power of producing vocal tones can only be acquired by attention to the muscular sensations; and the result of this is very imperfect.—The vocal sounds produced by the action of the larynx, are of very different characters; and may be distinguished into the *cry*, the *song*, and the ordinary or acquired *voice*. The *cry* is generally a sharp sound, having little modulation or accuracy of pitch, and being usually disagreeable in its 'timbre' or quality. It is that by which animals express their unpleasing emotions, especially pain or terror; and the Human infant, like many of the lower animals, can utter no other sound. In *song*, by the regulation of the vocal cords, definite and sustained musical tones are produced, which can be changed or modulated at the will of the individual. Different species of Birds have their respective songs; which are partly instinctive, and partly acquired by education. In Man, the power of song is entirely acquired; but some individuals possess a much greater facility in acquiring it than others; this superiority appearing to depend on their more precise conception of the tones to be sounded, and on their power of more ready imitation, as well as on differences in the construction of the larynx itself. The larynx of an accomplished vocalist, obedient to the expression of the emotions, as well as to the dictates of the will, may be said to be the most perfect musical instrument ever constructed. —The *voice* is a sound more resembling the cry, in regard to the absence of any sustained musical tone; but it differs from the cry, both in the quality of its tone, and in the modulation of which it is capable by the will. The power of producing *articulate* sounds, from the combination of which *Speech* results, is altogether independent of the larynx; being due to the action of the muscles of the mouth, tongue, and palate. Distinctly articulate sounds may be produced without any vocal or laryngeal tone, as when we *whisper*; and it has been experimentally shown, that the only condition necessary for this mode of speech, is the propulsion of a current of air through the mouth, from back to front. On the other hand, we may have the most perfect laryngeal tone, without any articulation; as in the production of musical sounds, not connected with words.

CONCLUSION.

It scarcely appears fitting to bring to a close this general survey of the Organised Creation, without the remark, that if little has been said in the course of it, upon the Evidences of Design presented by the structure of Living Beings, it is because it has been thought, that, when the perfect adaptation which exists between all their minute details, and the harmony of the parts they have to perform in the grand system of the Universe, were being explained and demonstrated, it might be safely left to the mind of the reader to draw those inferences, which it is perhaps impossible for any soundly-judging person to avoid making, who is unwarped by the pride of human reason, or by that tendency to practical disregard of them, which, in so many instances, is mistaken for a valid argument on the side of disbelief. When we consider the universality of this adaptation, so constant that it cannot be the effect of chance,—and the consummate harmony of the whole result, so immeasurably transcending the highest efforts of human genius,—it seems scarcely possible to arrive at any other rational conclusion, than that the Universe, with all that it contains, is the work of one Almighty and Benevolent Mind.

All our Science, then, is but an investigation of the mode in which the Creator acts; its highest 'laws' are but expressions of the mode in which He manifests His agency to us. And when the Physiologist is inclined to dwell unduly upon his capacity for penetrating the secrets of Nature, it may be salutary for him to reflect, that, even should he succeed in placing his department of study upon a level with those Physical Sciences, in which the most complete knowledge of 'causation' (using that term in the sense of 'unconditional sequence') has been acquired, and in which the highest generalizations have been attained, he is still as far as ever from being able to comprehend that Power, which is the 'efficient cause' alike of the simplest and most minute, and of the most complicated and most majestic phenomena of the Universe. But when Man shall have passed through this embryo state, and shall have undergone that metamorphosis, in which everything whose purpose was temporary shall be thrown aside, and his permanent or immortal essence shall alone remain, then, we are encouraged to believe, his finite mind will be brought into nearer connection with the Infinite, and his highest aspirations after Truth, Beauty, and Goodness will be gratified by the disclosure of their Source, and by the increase of his power of approach towards it. The Philosopher who has attained the highest summit of mortal wisdom, is he who, if he use his faculties aright, has the clearest perception of the limits of human knowledge, and the most earnest desires for the lifting of that veil which separates him from the Unseen. He, then, has the strongest motives for that humility of spirit and purity of heart, without which, we are assured, none shall see God.

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THE END.

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